THE INTER-RELATIONSHIPS OF THE BRYOPHYTA

By FRANK CAVERS, D.Sc., F.L.S.,

Lecturer in Botany at the School of Pharmacy and at Goldsmiths' College, University of London.

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PREFACE.

The present work is to a large extent a critical summary of the present state of knowledge and opinion in regard to the morphology and phylogeny of the Bryophytes, but the author has occasionally drawn upon the unpublished results of his own researches (in which he has been assisted by a Royal Society Grant) during recent years. The liverworts have been treated at considerably greater length than the Mosses, since they offer a field of wider interest to the morphologist. It is hoped that the work may be of use to students and perhaps of some value to investigators of these groups.

The author desires to express his deep indebtedness to Professor J. Bretland Farmer, F.R.S., of the Royal College of Science, under whom he began the study of botany, and whose lectures on Bryophytes, given in 1900, led the author to the further study of these fascinating plants.

F.C.

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THE INTER-RELATIONSHIPS OF THE BRYOPHYTA.

INTRODUCTION.

IN the present series of articles the writer proposes to give a summary and discussion of the morphology and affinities of the Bryophyta, together with lists of literature, which it is hoped may be of use to students interested in the group. For details and figures, since no attempt at completeness will be made here, reference should be made to the well-known works of Campbell ("Mosses and Ferns"), Goebel ("Organography of Plants"), and Lotsy ("Vorträge über botanische Stammesgeschichte," Band 2).

With some exceptions, the classification adopted in the "Pflanzenfamilien" of Engler and Prantl will be followed. The commonly accepted division of the Bryophyta into Hepaticæ (Liverworts) and Musci (Mosses) has, however, been challenged by several recent writers. The anomalous position of the Anthocerotales among the Hepaticæ was recognized by Leitgeb in his classical work ("Untersuchungen über die Lebermoose"). Gayet, in a paper on the development of the Bryophyte archegonium (which will be referred to later), definitely proposed to raise this family to the rank of a class co-ordinate with the Hepaticæ and the Musci, and Howe (18) first defined this class and named it the Anthocerotes. The propriety of this three-fold division of the Bryophyta will be discussed when the Anthocerotales are dealt with.

I.—SPHÆROCARPALES.

Setting aside the Anthocerotales, or Anthocerotes, for the present, the Hepaticæ have generally been divided into Marchan-

tiales and Jungermanniales. In the Marchantiales the plant-body is invariably a thallus of simple external form. The growing-point consists of a group of initial cells; when apical branching is about to occur, the group broadens out, the middle region grows forward and its cells stop dividing, and we get two growing-points separated by a "middle lobe." The apical branching is usually "dichotomous," owing to equal or sub-equal growth of the two new growing-points. Apart from the erect gametophores of the higher forms, the branches of the thallus grow solely in the horizontal plane, whether they are formed by "dichotomy" of the growing-point or arise laterally from the underside of the "midrib," and the margins are entire. Throughout the group, however, the thallus tissue is differentiated (except in the genera *Monoclea* and *Dumortiera*) into an upper zone of green tissue with air-chambers, opening by pores on the surface, and a lower zone of compact colourless tissue which serves for food-storage, frequently contains fungal hyphae, and is sometimes traversed by sclerotic fibres or by mucilage ducts. The lower surface bears scales and two kinds of rhizoids; of these some spring from the bases and the axils of the scales (which are typically arranged in two longitudinal rows), are provided with short peglike internal thickenings of the cell-wall (tuberculate rhizoids), and run back parallel with the underside of the thallus, while the others have smooth walls, have no relation to the scales, and grow directly downwards into the substratum. The sexual organs are either scattered over the thallus and separately embedded in it, or are collected into groups (receptacles) which are either sessile or stalked. The antheridium consists at an early stage of a row of cells, owing to repeated transverse divisions taking place in the mother-cell anterior to the formation of the first vertical walls. The archegonium neck consists of six rows of cells. The embryo sporophyte typically shows an octant stage; the mature capsule has (except in *Monoclea*) either no seta or a very short one; the capsule wall consists of a single layer of cells, and it opens in various ways but probably never splits into four equal valves. The spore mother-cell does not (except in *Targionia* and *Monoclea*) become four-lobed.

In the Jungermanniales, the plant-body is, in the vast majority of cases, differentiated into a cylindrical stem and two or three rows of leaves (one cell in thickness, with rare exceptions). When it is thalloid, it never has air chambers, but it shows a great variety of form and mode of branching, with a strong tendency to the

formation of simple or branched lobes or leaves. Apical growth is always effected by a single apical cell; in the leafy forms this cell is generally a three-sided pyramid, in the thalloid forms it varies in shape. In apical branching, the apical cell of the branch is constituted of a segment cut from the parent apical cell, and the branching is typically monopodial. There are no tuberculate rhizoids. The sexual organs are usually developed in groups, but never on special stalked receptacles. In the young antheridium vertical divisions set in at a very early stage, usually after a single transverse division of the mother-cell. The neck of the archegonium consists of five rows of cells. The embryo typically divides by repeated transverse walls, the lower (hypobasal) of the two cells formed by the first division usually taking no further part in the development of the sporophyte; there is no octant stage. The sporogonium usually has a relatively long seta, and the capsule nearly always opens by four valves, never by a lid. The spore mother-cell becomes deeply four-lobed before the tetrad division occurs.

Though these two groups are, on the whole, sharply distinguished, there are interesting cross-affinities between the lowest members of the two groups. The Ricciaceæ, the lowest of the Marchantiales, present the simplest type of sporophyte, in which sterilisation is (except in *Tessellina*) confined to a single peripheral layer of cells, forming an epidermis or capsule-wall around the wholly sporogenous central tissue. In this respect the Ricciaceæ are sharply marked off from all other Bryophytes, but in the structure of the thallus and of the sexual organs they agree closely with the higher Marchantiales.

The small families Sphærocarpoideæ and Rielloideæ, which Schiffner (27) places at the base of the Jungermanniales, are regarded by Goebel and by Lotsy as belonging to the Marchantiales, and as a matter of fact they were included in the Ricciaceæ by the earlier systematists. These two families agree with the Jungermanniales in having no air-chambers in the thallus, in having no tuberculate rhizoids, and in showing a marked tendency towards the development of leaves; but they agree with the Marchantiales in the development of the sexual organs, in the early stages of embryogeny, and in having a single-layered capsule wall. Finally, they show certain peculiarities not found elsewhere in the Liverworts—the special envelope around each antheridium and archegonium in both families, and the curious wing of *Riella*. It would seme

advisable, if these families must be removed from the Jungermanniales, to place them in a special group—for which the name *Sphærocarpales* is suggested—quite independent of the Marchantiales and the Jungermanniales, though showing affinities with both of these groups.

Were we to take the further step of transferring the Ricciaceæ from the Marchantiales and uniting them with the Sphærocarpales, we should have a synthetic generalised group which would practically realise our conception of the common ancestral stock from which were probably derived the Marchantiales and the Jungermanniales. But the affinities of the Ricciaceæ with the higher Marchantiales are so close, especially when we take into account the transitional group Corsiniaceæ, that such a step hardly seems justifiable. However, starting from a hypothetical ancestral form (Lotsy's " Sphæro-riccia ") with the simple type of thallus found in *Sphærocarpus* (but without the envelopes of the sexual organs) and the simple sporophyte of a *Riccia*, the evolution of the Hepaticæ (excluding the Anthocerotales) may readily be regarded as having proceeded along two diverging lines. The *Marchantia* line is marked by elaboration in the internal structure of the thallus and by the aggregation of the sexual organs into receptacles of increasing complexity; while the *Jungermannia* line shows external differentiation of the plant-body, leading to the typical leafy Acrogynæ, the internal structure of the vegetative organs remaining in most cases simple, though the capsule attains greater specialisation in internal structure than in the Marchantiales.

SPHÆROCARPACEÆ.

The Sphærocarpales may be divided into two orders—the Sphærocarpaceæ with two genera (*Sphærocarpus, Geothallus*) and the Riellaceæ with the single genus *Riella*.

The most striking features of the Sphærocarpales are the presence of a special envelope around each antheridium and archegonium ; the absence of typical elaters, which are represented only by sterile archesporial cells mixed with the spores ; the feeble development of the sporogonial seta ; and the absence of fibrous thickenings from the single-layered capsule wall, which merely decays to set the spores free.

Most species of *Sphærocarpus* have a very simple thallus, with notched margins, each notch marking the position of a growing

point with an apical cell from which segments are cut off above and below, as well as laterally. The thallus consists almost entirely of uniform green cells, arranged in several layers at the middle, where it is attached to the soil by rhizoids, and thinning out to a single layer at the margins. At the growing points, there are, especially on the underside, mucilage-hairs consisting of a row of cells, the terminal cell being large and club-shaped. Petounnikow (25), who, in 1867, discovered the male plants of *Sphærocarpus*, regarded these hairs as rudimentary leaves, corresponding to the

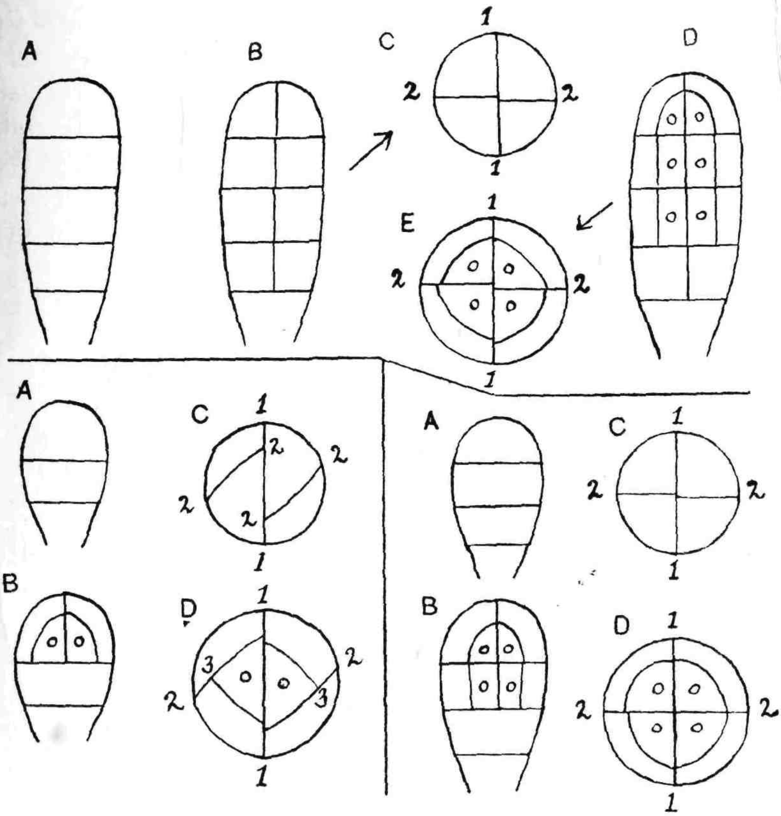


Fig. 1. Diagrams illustrating the early development of the Antheridium
bern Marchantiales (upper row), Sphærocarpales (lower row, right), and
germanniales (lower row, left); cross-sections shown in C and E of upper
*Sph*s, and in C and D of lower series
inte
In G al scales of the Marchantiales and the amphigastria or under
of th s of the Acrogynæ, and there is abundant evidence for the

view that leaves have arisen, in various groups of Liverworts, from mucilage-hairs primarily adapted for protection of the growing apex. Campbell (4) discovered in plants of *S. californicus*, growing in unusually moist and shaded places, regular marginal lobes or leaves comparable with those of *Blasia* or *Fossombronia*.

The genus is diœcious, the male plants being extremely small, (usually little more than 0·1 mm. in diameter) and often covered by the larger female plants. The development of the antheridium is interesting, since it forms a type intermediate between those observed in the Marchantiales and the Jungermanniales (Fig. 1.) The mother-cell divides transversely; the basal cell undergoes no further division, but the upper divides to form three superposed cells; of these the lowest divides again to form the short stalk, while vertical walls appear in the two upper cells, giving an octant stage. In each of the eight cells a periclinal wall is then formed, cutting off a wall-cell from a primary sperm-cell. The body of the ripe antheridium is spherical. The surrounding cells of the thallus grow out to form an envelope which extends far beyond the antheridium itself and becomes flask-shaped (Fig. 2,A).

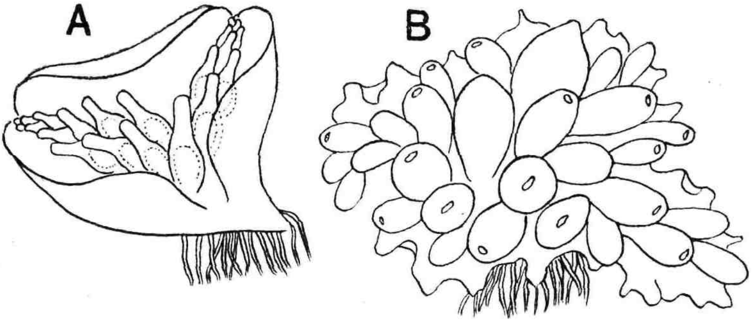


Fig. 2. *Sphærocarpus terrestris.* A, a male plant, × 40; B, a female plant, × 10.

The archegonium shows the typical Liverwort development, fully described by Campbell (3). When mature, it is sessile, and its neck consists of six rows of cells, with an axial row of four canal cells; it should be noted that the archegonium of the Sphærocarpales exactly resembles that of the Marchanti[...] erely whereas in Jungermanniales there is usually a stalk and are five rows of neck-cells. The neck is strongly curved forv[...] with as is the envelope which grows up around the archegonium (Fig[...] The envelope develops independently of fertilisation, and [...]owing

invests the archegonium; like that of the antheridium, it consists of a single layer of cells.

The embryogeny is of the Marchantiales type, the first (basal) wall being transverse, and the lower cell giving rise to the foot of the sporogonium, which is separated from the spherical capsule by a short neck-like seta. The archesporial cells at first contain chloroplasts and starch-grains, but after a time these are replaced by oil-drops in certain cells, and these cells give rise to the spores. The spore mother-cells are spherical and do not become lobed before the tetrad division; in this respect *Sphærocarpus* differs from the Jungermanniales and resembles the Marchantiales. The sterile cells retain their starch, and according to Leclerc du Sablon (21) they resemble the spore mother-cells in the division of the nucleus into four; they become ovoid in form and are used up by the developing spores. The calyptra, formed from the venter of the archegonium, is ruptured by the increase in volume of the ripening capsule, and the spores are set free by the decay of the capsule wall and of the envelope. In *S. terrestris* the four spores of the tetrad remain united within a common outer spore-coat, and as has been shown by Douin (11) and by Strasburger (32), of the four resulting plants, two are commonly male and two female. In *S. Donnellii*, however, the four spores separate when mature, and in *S. cristatus* the spores separate long before the capsule ripens.

Geothallus, discovered and described by Campbell (5, 6), is a Californian genus closely allied to *Sphærocarpus*, from which it differs in being a much larger plant and in the definite organisation of leaves. Moreover, the plant is perennial, and at the beginning of the dry season the younger part of the axis is converted into a tuber in which food is stored up, the apex persisting and resuming growth with the return of favourable conditions. The sexual organs and sporogonium are very similar to those of *Sphærocarpus*, and the chief interest of the genus centres in the differentiation of the plant body into axis and leaves. A leaf is formed from each lateral segment cut from the apical cell. The leaves are at first placed vertically, but later become shifted so as to be "succubous" (*i.e.*, the hinder edge of each leaf overlaps the anterior edge of the leaf behind it) or horizontal. This marks a great advance upon *Sphærocarpus*, in which the leaves are simply wings of the thallus interrupted by the notches in which the growing-points are situated. In *Geothallus*, leaf-like outgrowths also arise from the upper surface of the axis, and sometimes these are continuous with the lateral

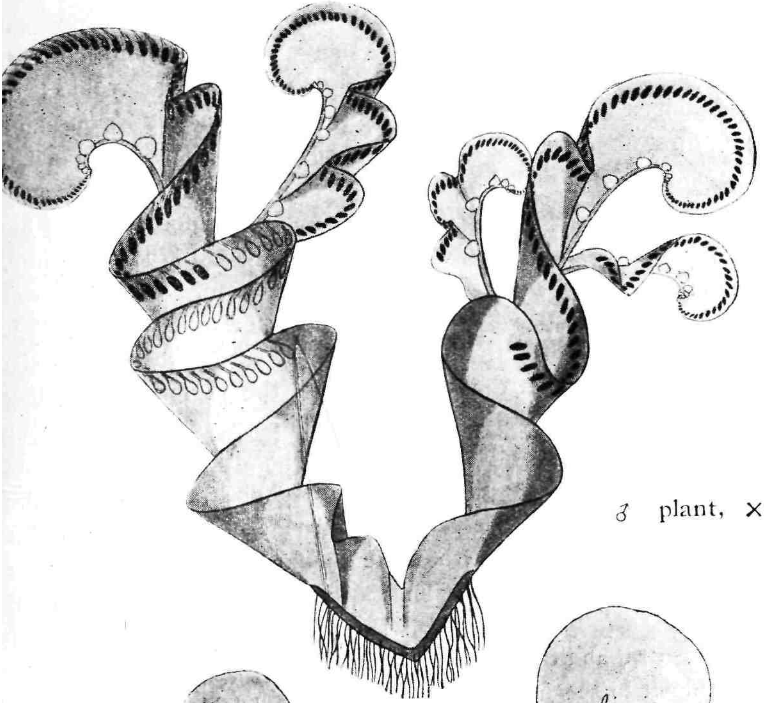
leaves. A similar arrangement occurs in the genus *Petalophyllum*, and this, together with the tuber formation which occurs in both genera, led Goebel (13) to the view that *Geothallus* is closely allied to *Petalophyllum*; but we meet with the same thing again in a species of *Anthoceros*, and it is obviously nothing more than a case of homoplasy—which, as has been pointed out by Farmer and by Goebel, the Hepaticæ show to an extent that cannot be paralleled by any other group of plants.

RIELLACEÆ.

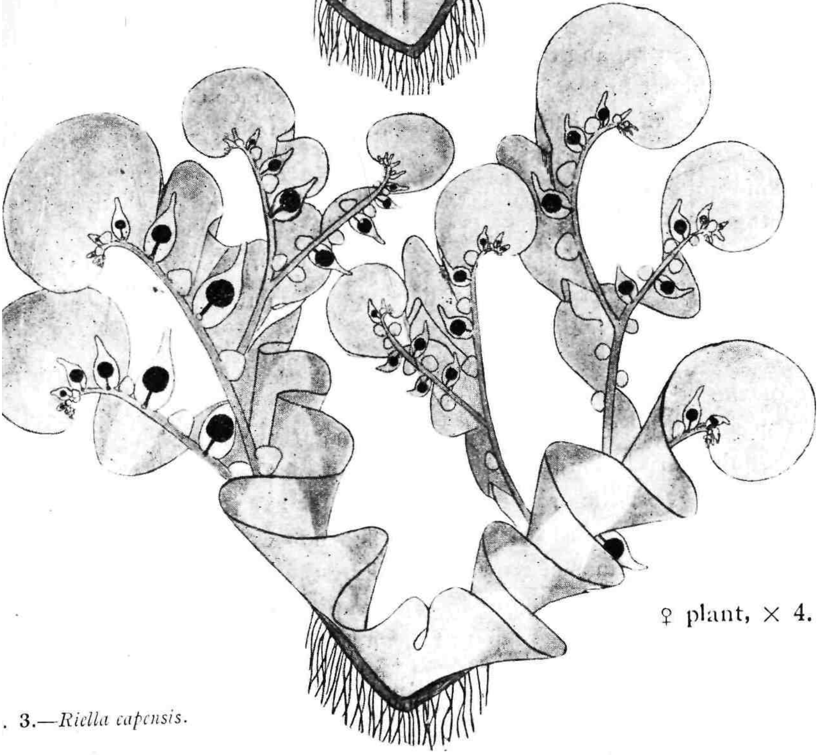
Until 1902 the remarkable aquatic genus *Riella* was supposed to be confined to the Mediterranean basin, the seven species then known have been recorded from Algeria, France, Sardinia, and the Lake of Geneva (*R. Reuteri*, described by Hofmeister, but long ago destroyed owing to the erection of a mill on the lake-side). New species have since been described from Turkestan by Porsild (26), from Texas and the Grand Canary by Howe and Underwood (19), and from Port Elizabeth, South Africa, by the writer (7)—*R. capensis* is of interest as extending the range of the genus to the Southern Hemisphere. A paper on *R. capensis*, and on the genus generally, is being prepared for publication.

Riella closely resembles *Sphærocarpus* and *Geothallus* in the structure of the sexual organs and sporophyte, but differs greatly from these genera in having a cylindrical axis or stem which is produced dorsally into a wing-like expansion, besides bearing a row of leaves on either side at the base of the wing. In *R. bialata*, recently described by Trabut (37), there are two wings, right and left, both arising from the dorsal side of the stem.

The morphology of *Riella* has been much discussed. Several writers have doubted the accuracy of Montagne's original description and figure (1, 2) of *R. helicophylla*, the first species to be discovered, in which the wing was represented as being wound in a close spiral, like the thread of a screw, around the erect stem. Leitgeb (22) confirmed this description, found that the cells of the axis showed spiral twisting, and suggested that the wing arose at a late stage, after the stem had coiled around some supporting water-plant; this suggestion of a climbing habit was quite erroneous, but Leitgeb had only herbarium material. Later writers supposed that the spiral appearance of the wing was simply an optical illusion, and that the wing was merely folded and wavy, as is certainly the case in *R. capensis* (Fig. 3). Quite recently, however, *R. helicophylla* has



♂ plant, × 4.



♀ plant, × 4.

3.—*Riella capensis.*

been again examined by Porsild (26) and by Müller (24), and it would appear that Montagne's account of this species was quite correct.

The nature of the wing itself has formed the subject of conflicting statements. Hofmeister (17) compared the *Riella* plant to a *Marchantia* or a *Metzgeria* in which the thin lateral wing had developed only on one side of the midrib, and Goebel has recently adopted this explanation in a somewhat modified form, basing his interpretation chiefly on observations made with young plants. Goebel's "Profilstellung" theory of the organisation of *Riella* assumes that this genus differs from all other Liverworts in that the development of the thallus is in the vertical instead of in the horizontal plane; that the whole tissue of the young plant arising from the spore is at first meristematic and consists of a single layer of cells; that later an intercalary growing-point arises either at one place or at two opposite places on the margin of the plate; that the new cells formed on the upper or distal side of the growing-point then contribute to the growth of the one-layered wing, while those formed on the lower or proximal side go to form the cylindrical stem. Solms (30), however, upholds Leitgeb's view that the plant is dorsiventral and that the wing is simply a dorsal outgrowth; and it is difficult to see how Goebel's explanation could be applied to the case of *R. bialata*. The extreme plasticity of the Hepatic plant-body renders elaborate interpretations of the "Profilstellung" kind quite unnecessary, just as this plasticity completely baffles the attempt sometimes made to distinguish between "thallus-lobes" and "leaves" in this group. Schiffner (29) has described and figured the occurrence of leaf-like organs on the marginal portion of the wing in *R. Battandieri*.

A comparison of the descriptions and figures in the literature of the genus, and the examination of specimens of most of the species hitherto discovered, shows that there is on the whole a definite correlation between the breadth of the wing and the size of the leaves; the broader the wing, the smaller are the leaves, and *vice versâ*. The form of the plant depends very largely upon the external conditions of growth, especially the depth at which it grows in the water and the light which falls upon it. Most of the species grow erect in fairly deep water, and have a broad wing, usually thrown into folds, and relatively small leaves; these erect species are attached to the mud by rhizoids at the base of the stem. Some species, growing in shallow water, have a creeping stem, attached along its whole length by rhizoids; here the leaves are relatively

large and the wing narrow. The same is the case in *R. Clausonis*, which has unusually large leaves, while the narrow wing remains undeveloped in places, and rhizoids are absent; this species frequently floats on the surface of ponds. Corbière (8) observed that plants of *R. gallica* which had been stranded on mud, owing to the drying of the pond, were attached by means of rhizoids given off all along the stem; he regards this plant as merely a variety of *R. Battandieri*, which grows erect in water.

The antheridia are produced on the free edge of the wing and become enclosed separately in pockets formed by local thickening of the otherwise one-layered wing. The archegonia, each surrounded by a flask-like envelope, which is smooth in some species, but in others has eight longitudinal folds, are developed on the stem at the base of the wing; some species are diœcious, others monœcious.

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II.—MARCHANTIALES.

This group, as already defined, is divided by Schiffner, Müller, and other systematists, into two orders, Ricciaceæ and Marchantiaceæ.

In the Ricciaceæ, which includes the two genera *Riccia* and *Tessellina*, the green upper zone of the thallus consists either of erect filaments separated by narrow air-spaces, or of a network of lamellæ which are generally roofed over to form wide chambers; in the latter case, however, the chambers are devoid of special assimilating outgrowths. The air-pores are surrounded by a single ring of cells. Ventral scales are generally present, but are often small, and never show differentiation of an appendage. The sexual organs are developed singly and each becomes deeply embedded in the thallus; the canal of the antheridial cavity is often prolonged into a conical or cylindrical ostiole, and the archegonium neck is generally exserted from the archegonial cavity. The sporophyte is a simple spore-fruit or capsule, without seta or foot; sterilisation is limited to the production of a single-layered wall. The capsule remains enclosed in the calyptra, and the spores escape by decay of the capsule wall, the calyptra, and the surrounding tissue of the thallus.

In the Marchantiaceæ, the green zone of the thallus consists of well-developed air-chambers (except in *Dumortiera* and *Monoclea*), which generally either contain loose filamentous assimilating tissue or are divided into secondary chambers by chlorophyll-bearing lamellæ. The air-pores are surrounded by a single ring, or by several concentric rings, or by several superposed rings, of modified epidermal cells. The sexual organs are nearly always aggregated into receptacles, or gametophores; in all except the lowest forms the archegoniophores are stalked, as are also the antheridiophores in the highest forms. The sporophyte is differentiated into foot, seta, and capsule, and the latter is when ripe pushed through the calyptra; except in *Corsinia* the sterile inner cells of the capsule are developed as elaters with fibrous thickenings.

Since the publication of Schiffner's classification of the Marchantiales, considerable additions have been made to our knowledge of the group, and on various grounds it seems necessary to propose certain modifications in Schiffner's scheme. Schiffner

divides the Marchantiaceæ into three sub-orders—Corsinioideæ, Targionioideæ, and Marchantioideæ. These, it is now suggested, should be raised to the rank of orders. There is no sharp distinction between the Ricciaceæ and Schiffner's Marchantiaceæ, except in the structure of the sporophyte, and even in this respect *Tessellina* shows an approach to a connecting link between the two groups. At any rate, it seems hardly justifiable to set the Ricciaceæ against the whole of the remaining Marchantiales. The genus *Monoclea*, which must now be removed from the Jungermanniales, should in the writer's opinion be placed in an order (Monocleaceæ) by itself, standing between the Corsiniaceæ and the Targioniaceæ. With the Marchantiaceæ in the restricted sense (corresponding to Schiffner's Marchantioideæ), we thus get five orders of Marchantiales.

RICCIACEÆ.

In most species of *Riccia* the upper zone of the thallus consists of narrow vertical air-canals, each bounded by four of the filaments produced by outgrowth and repeated transverse division of a superficial cell. The terminal cell of each filament is usually larger than the rest, forming with the corresponding cells of the neighbouring filaments a sort of epidermis of hyaline cells containing few or no chloroplasts (Fig. 4). In many species, each of these epidermal

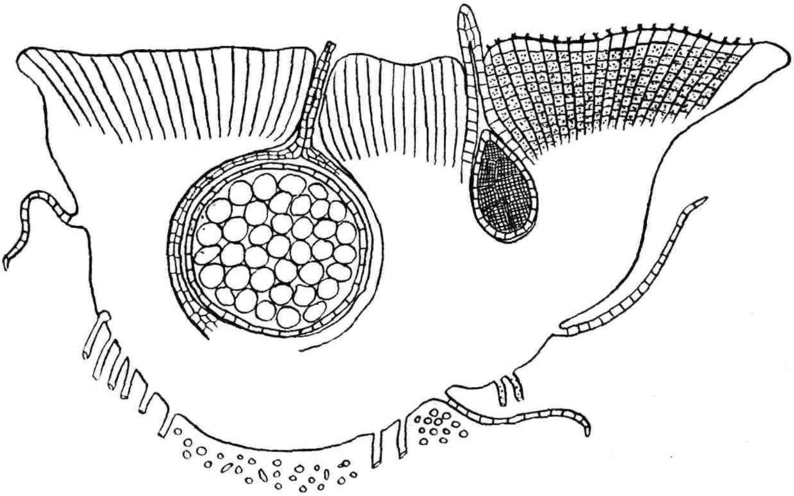


Fig. 4. *Riccia glaucescens.* Transverse section of thallus with an unripe sporogonium on the left and an antheridium on the right.

cells becomes divided into an upper and a lower cell, and the former eventually dries up and collapses, leaving only the lower part of its

wall as a cup. Sometimes each epidermal cell grows out into a long colourless hair.

In several species the air-canals become drawn out into wide chambers, bounded by cell-plates; these species have by different writers been separated under the name *Ricciella*, regarded by some as a sub-genus of *Riccia* and by others as an independent genus. In *R. crystallina*, which grows in very moist and shaded places, the wide chambers remain open above and form shallow cavities separated by a network of thin vertical partitions. In *R. fluitans*, the chambers are roofed over by a layer of cells; in sterile aquatic plants, which float just under the surface-film of the water, the chambers are closed, but in the land form a pore is left in the roof of each chamber. In some allied species, the chambers are partitioned up, so as to form two or more superposed tiers as seen in cross-section of the thallus. The figure given in various text-books as the land-form of *R. fluitans*, e.g., in Fig. 379 of the English edition of Strasburger's "Text-book of Botany," is in reality a representation of *R. natans*; the land form of *R. fluitans* differs from the water-form only in having rhizoids, sexual organs and fruits, but not in the general habit of the thallus.

Riccia natans is also an amphibious species, and it too has been separated as a distinct genus, *Ricciocarpus*, but the recent investigation of this plant by Lewis (14) and by Garber (8) has shown

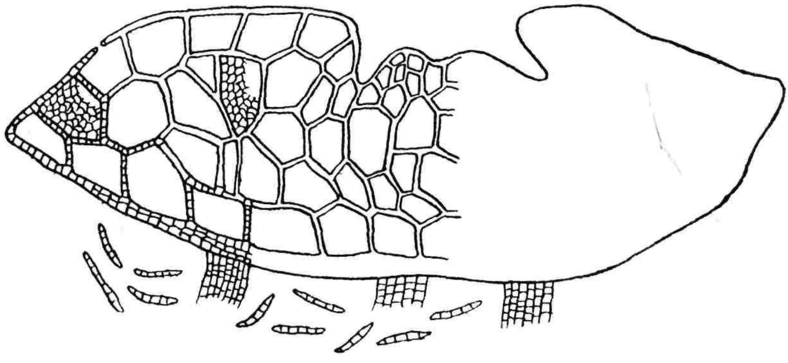


Fig. 5. *Riccia natans*. Transverse section of thallus showing air-chambers and ventral scales.

conclusively that the older systematists were correct in including it in the genus *Riccia*. The sterile free-floating aquatic form has a broad thallus, and the air-chambers are divided up by plates

of tissue, so that the thallus comes to consist almost entirely of a spongy mass, the compact ventral tissue being reduced to two or three layers of cells (Fig. 5). The ventral scales are long and narrow and are scattered over the whole underside of the thallus; they shew long-continued growth in length owing to the basal cells being meristematic. In the land-form, which Lindberg (Bot. Centralblatt, Band 6, p. 363) showed to be identical with *Riccia lutescens* (a fact recently discovered independently by Lewis), the thallus is of simpler structure and the scales are short and semilunar in shape. In the other species of *Riccia*, the scales are developed in a single series, but they usually become split in the middle, giving rise to two lateral rows; in the hygrophilous species they soon perish, but in xerophilous species they are large and persistent.

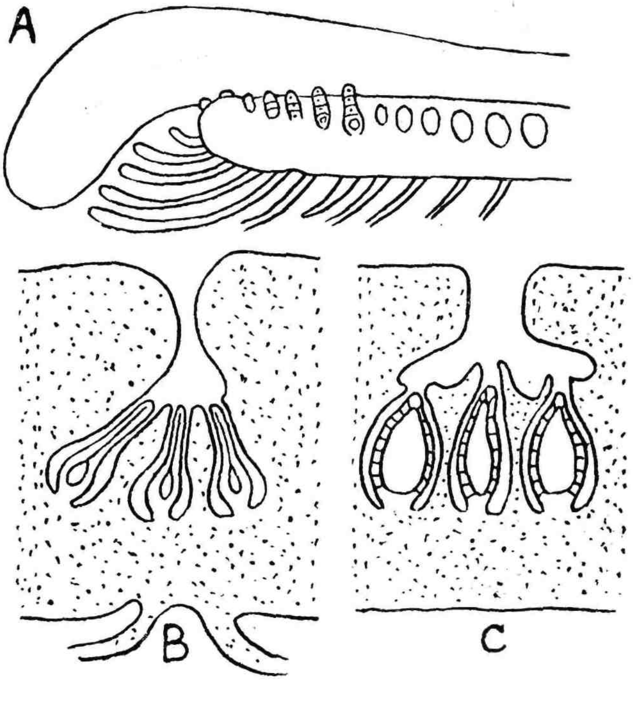


Fig. 6. *Riccia natans*. A, longitudinal section of thallus, showing antheridia and archegonia; B, transverse section of archegonium-bearing portion; C, transverse section of antheridium-bearing portion. After Garber.

The sexual organs are usually scattered, and sunk separately in deep cavities. In some species there is a tendency to the

aggregation of the antheridia into groups, and this is very pronounced in *R. natans*, in which these organs are developed in two or three rows on a long receptacle, forming a ridge with a groove on either side and arched over by the neighbouring tissue of the thallus (Fig. 6).

In *Tessellina* (Fig. 7), the air-chambers are arranged in a single

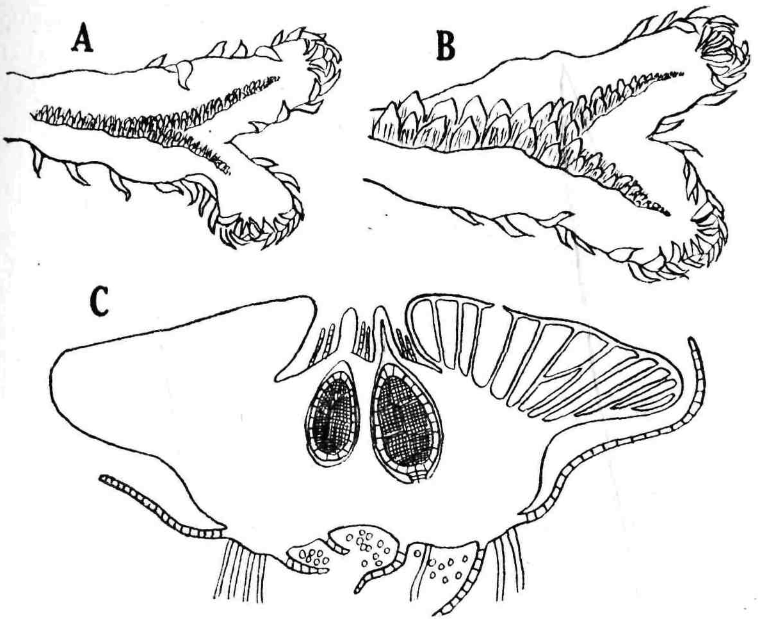


Fig. 7. *Tesselina pyramidata.* A, a male plant, × 2 ; B, a female plant, × 2 ; C, transverse section of a male plant, showing two antheridia.

series, and each opens by a pore which is raised above the surface of the thallus and surrounded by five or six cells with strongly thickened radial walls. The ventral scales arise in two independent rows, as in the higher Marchantiales. The antheridia are in groups, marked by tufts of hairs among which arise the cylindrical ostioles of the antheridial chambers. In the female plant, each archegonium becomes surrounded by a conspicuous green conical outgrowth containing air-chambers. As was shown by Leitgeb, the capsule contains rounded sterile cells, but since these lie just within the capsule-wall, it is doubtful whether they can be regarded as sterile archesporial cells. Leitgeb[1] thought these sterile cells represented

[1] Untersuchungen, IV., p. 45.

a rudimentary doubling of the normally single-layered wall of the fruit, but throughout the Marchantiales the capsule-wall consists of a single layer of cells, except for the apical thickened cap frequently found in the higher families. Hence the interpretation of these sterile cells in *Tessellina* remains an open question.

CORSINIACEÆ.

In the two genera belonging here, the archegonia are developed in sunken groups on the upper side of the thallus, each group being protected by the outgrowth of the thallus-tissue; the capsule is separated from the foot by a short neck-like seta, and its wall becomes disorganised to set the spores free. The air-chambers are arranged in a single layer, and each chamber opens by a pore surrounded by a single ring of cells.

In *Corsinia* the cells forming the floor of the chambers generally grow out to form short assimilating filaments, but sometimes these are wanting. The ventral scales are small and are scattered over the whole underside of the thallus, as in *Riccia natans*; each scale has on its free margin a long threadlike appendage, and at the front of the thallus these appendages bend up over the growing-point, in the same way as the more highly developed appendages characteristic of the ventral scales of the higher orders of Marchantiales.

The antheridia are collected into a receptacle which has the form of a ridge, as in *Riccia natans*; sometimes it is forked in front owing to branching of the apex, but the growing-point of the thallus is not used up in the development of the receptacle, hence several receptacles may be formed one after another. Each archegonial group, containing from six to ten archegonia, accompanied by numerous hairs (paraphyses) lies in a depression of the thallus; several groups may be formed in succession, the growing apex not being used up. The developing sporogonium is protected by a curious involucre, which grows up from the depression and becomes lobed, the lobes containing air-chambers (Fig. 8). This outgrowth is not fully formed unless fertilisation occurs; if only one archegonium develops a fruit, the involucre bends over it and shows one-sided growth, becoming palmately lobed, but if several fruits are formed, the outgrowth becomes radially symmetrical and peltate, its lobes covering the developing fruits. The capsule contains numerous sterile cells mixed with the spore mother-cells, but neither these cells nor those forming the capsule-wall bear fibrous hickenings (Fig. 9).

Corsinia, though showing distinct affinities with the Ricciaceæ, makes some important advances upon that family, especially in the more definite organisation of the receptacles, or gametophores, and

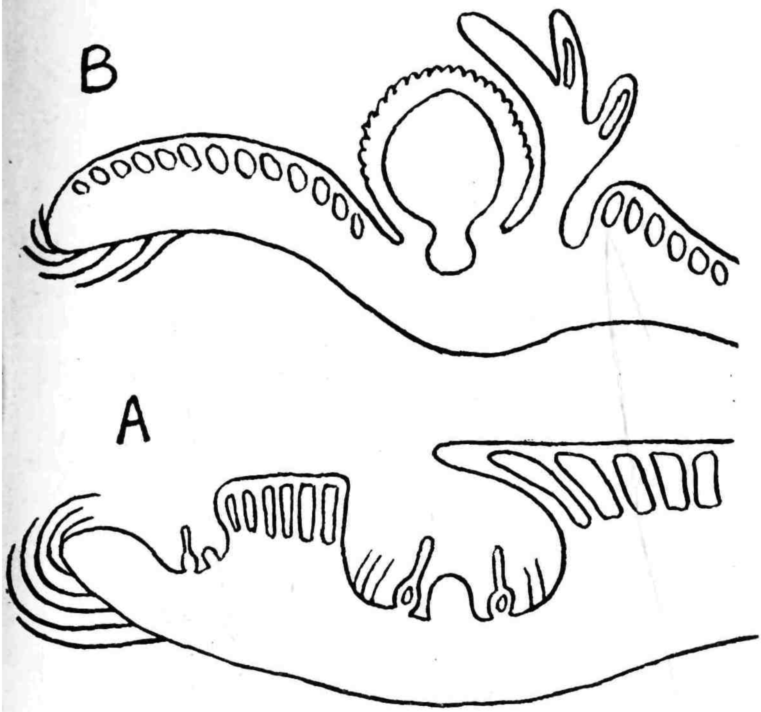


Fig. 8. *Corsinia marchantioides*. Longitudinal sections of thallus. A, shows the outgrowth arising in the midst of the archegonial group; B, a later stage, with a young sporogonium. After Leitgeb.

the structure of the sporophyte, as well as in that of the thallus. ie curious outgrowth which arises in the midst of the archegonia ig. 8) foreshadows the elaborate archegoniophore, or carpophalum, of the higher Marchantiales.

Boschia, with a single species, is found only in Brazil; our owledge of this interesting plant is due to Leitgeb.[1] It has the bit of a xerophilous *Riccia*. The large two-rowed ventral scales ll up over the narrow thallus in the dry state; the air-chambers contain well-developed filaments. The antheridia are developed in row on the midrib of the male plant, but are not collected into a lefinite antheridiophore. The archegonia are produced in groups

[1] Unters, iv., p. 57.

of three or four, each group sunk in a cup-like depression

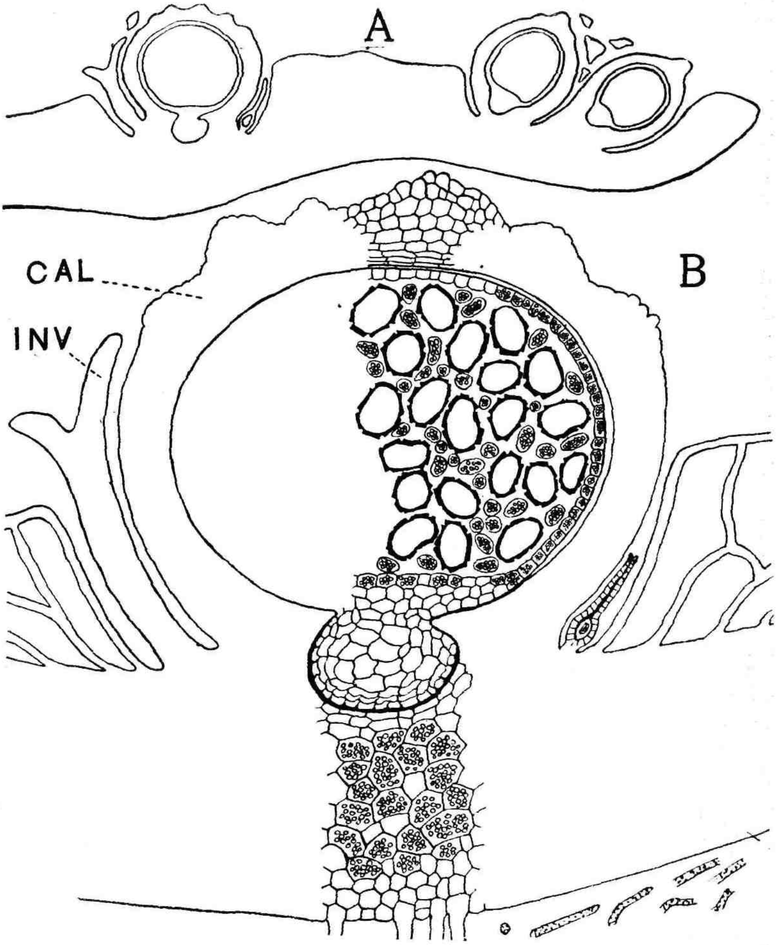


Fig. 9. *Corsinia marchantioides.* A, longitudinal section of thallus witl three sporogonia. B, a part of A enlarged; *in.*, involucre; *cal.*, calyptra mingled with the developing spores are the starch-bearing sterile cells.

Immediately behind the group there arises a hood-like outgrowt which bends forward over the archegonia (Fig. 10); this involucre i several cells thick but contains no chambers, and it is formed quite independently of fertilisation. The cells forming the capsule-wall are strengthened by U-shaped fibres deposited on the inner and radial walls; the sterile archesporial cells persist after the ripening of the spores and bear annular or spiral fibres, hence they are definite though short elaters.

Boschia lags behind *Corsinia* in the organisation of the sexual receptacles, but advances upon it in the structure of the thallus, of the capsule-wall, and of the sterile cells in the capsule.

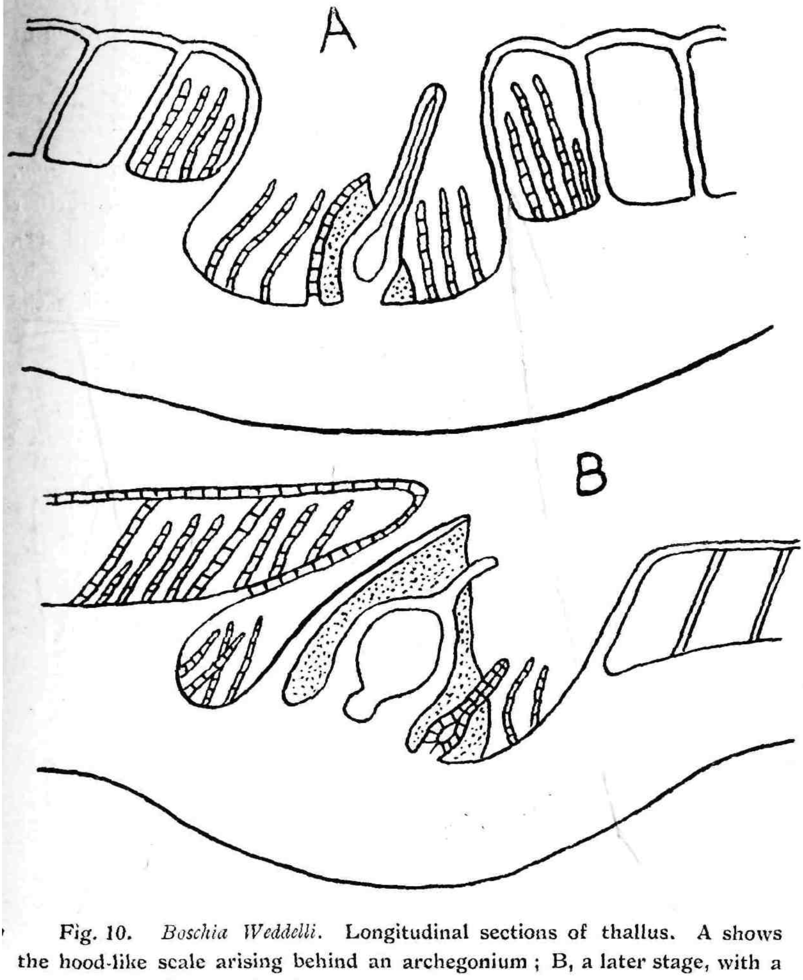


Fig. 10. *Boschia Weddelli.* Longitudinal sections of thallus. A shows the hood-like scale arising behind an archegonium; B, a later stage, with a young sporogonium. After Leitgeb.

This little group is of great interest, being transitional in various respects between the Ricciaceæ and the higher Marchantiales. One of the most interesting features is the formation of a special outgrowth for the protection of the young sporophyte. In the hood which arises behind the archegonial group in *Boschia* we have a structure which may be compared with the two-valved involucre of

the Targioniaceæ and with the tubular involucre of *Monoclea*; while the umbrella-like outgrowth of *Corsinia* represents, so to speak, a belated attempt at the formation of the stalked archegoniophore, or carpocephalum, of the Marchantiaceæ (Marchantioideæ), which arises in advance of the archegonia and carries them up with it owing to basal growth and also turns them upside-down owing to growth of its expanded upper portion.

TARGIONIACEÆ.

This order contains the two genera *Targionia* and *Cyathodium*. The development of both was worked out by Leitgeb; further investigations have been made on *Targionia* by Campbell (1), Macfadden (15), Cavers (3), and Douin (7), and on *Cyathodium* by Lang (13). The chief distinguishing features of the order are the

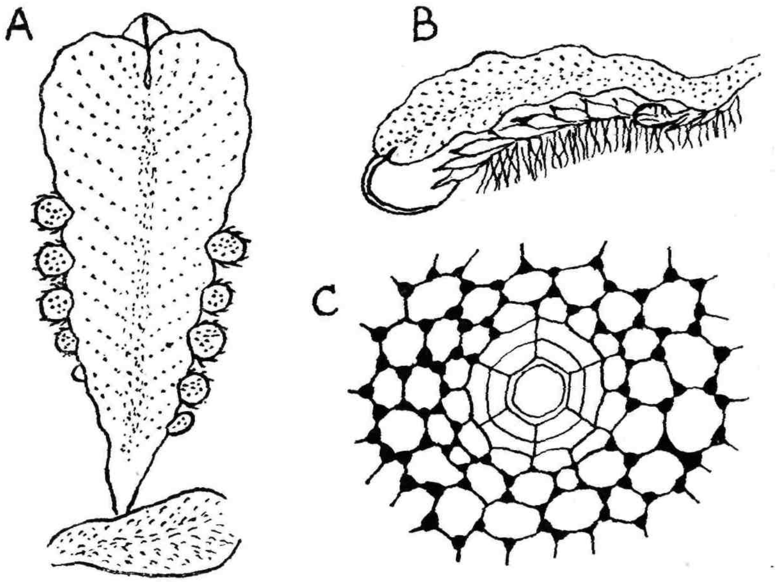


Fig. 11. *Targionia hypophylla*. A, a plant, seen from above, with male branches at the sides and an involucre at the apex; B, a similar plant in side view, showing the bivalved involucre; C, part of the epidermis, with an air pore in surface view.

restriction of the antheridia to special short ventral branches of the thallus, and the development of an envelope, consisting of two lateral scales, around the archegonial group. The latter occupies an area immediately behind the growing-point of the thallus, the

apical growth being arrested by the formation of the archegonia, so that further growth is only possible by means of adventitious branches.

In *Targionia* (Figs. 11, 12, 13) the air-chambers, arranged in a

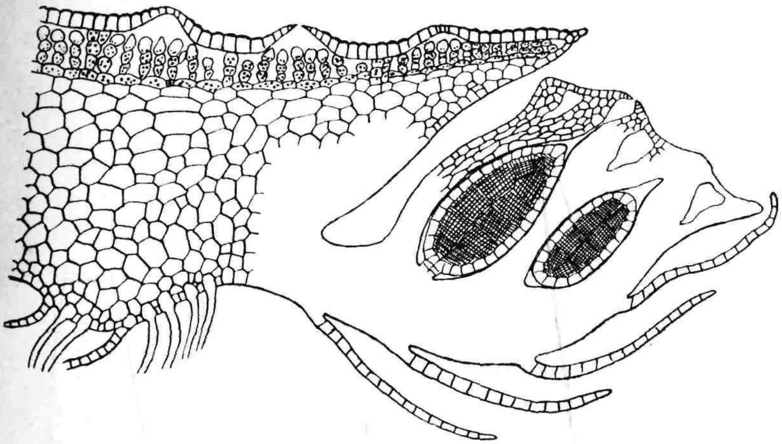


Fig. 12. *Targionia hypophylla.* Transverse section of thallus, with an antheridial branch on the right.

single layer, contain assimilating filaments, and the pore is surrounded by several concentric rings of cells. Each of the male branches, arising from the sides of the midrib, consists of a cylindrical basal portion and an expanded terminal receptacle. The upper surface of the latter is studded with little conical outgrowths, each traversed by a canal leading down to an antheridium-containing chamber (Fig. 12). The archegonia, formed just behind the growing-point of the thallus, are arranged in two longitudinal rows, and from either side of the group there arises a scale which grows forward and, meeting the opposite scale, forms a complete sheath over the developing sporogonium, the edges of the two scales becoming united by interlocking processes (Figs. 11, 13). The sporogonium consists of a spherical capsule, separated from the bulbous foot by a seta which eventually elongates, rupturing the calyptra and pushing apart the two halves of the involucre, exposing the upper portion of the ripe capsule in order that the spores may be dispersed. The cells forming the apical part of the capsule-wall are larger than the rest and have short elater-like cells attached to them, so that in this region the wall is two-layered, and at dehiscence

is detached as a lid. The elaters are well developed, mingled irregularly with the spores, and often branched. The spore mother-cells, instead of remaining spherical or ovoid as in the other Marchantiales (except *Monoclea*), become deeply divided into four lobes (as in Jungermanniales).

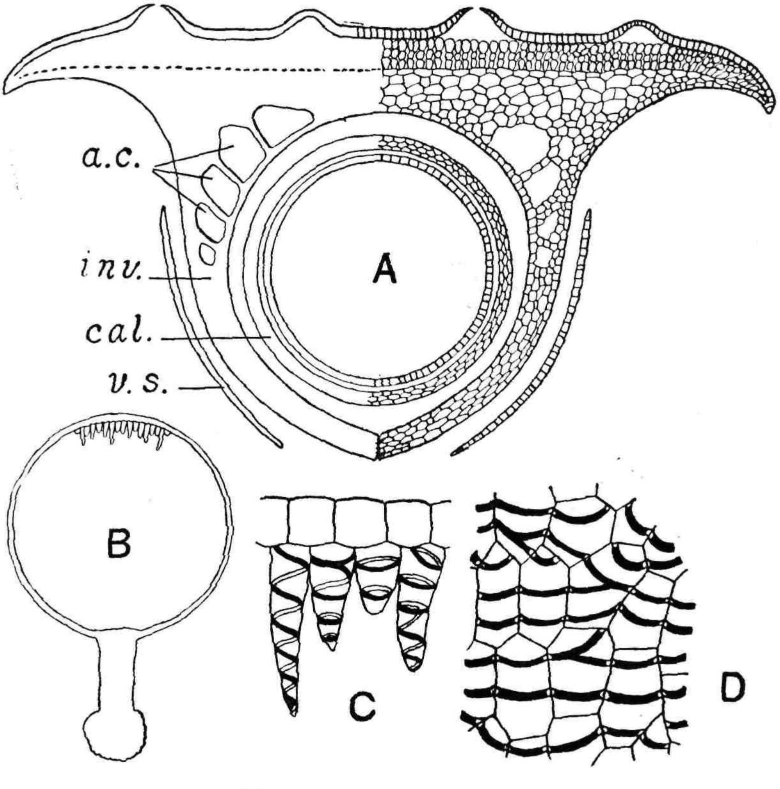


Fig. 13.—*Targionia hypophylla.*

Fig. 13. A.—Transverse section across the anterior end of a fruiting plant, showing a nearly mature sporogonium enclosed in its calyptra (cal.) and surrounded by the two-lobed involucre (inv.), the tissue of which contains air-chambers at the base (a.c.). Outside of the involucre, two ventral scales (v.s.) are shown. The upper part of the section shows the ordinary structure of the thallus. ×35. B.—Median longitudinal section of a nearly mature sporogonium, showing the spherical capsule, short seta, and bulbous foot. The spores and elaters are omitted, to show more clearly the apical patch of fixed elater-like cells. ×35. C.—Part of B., showing some of the elater-like cells at the apex of the capsule. ×300. D.—Part of the ripe capsule-wall, showing the annular fibrous bands on the walls of the cells (surface view). ×300.

Cyathodium is closely allied to *Targionia*, and the structural differences in the thallus which separate the two genera are chiefly

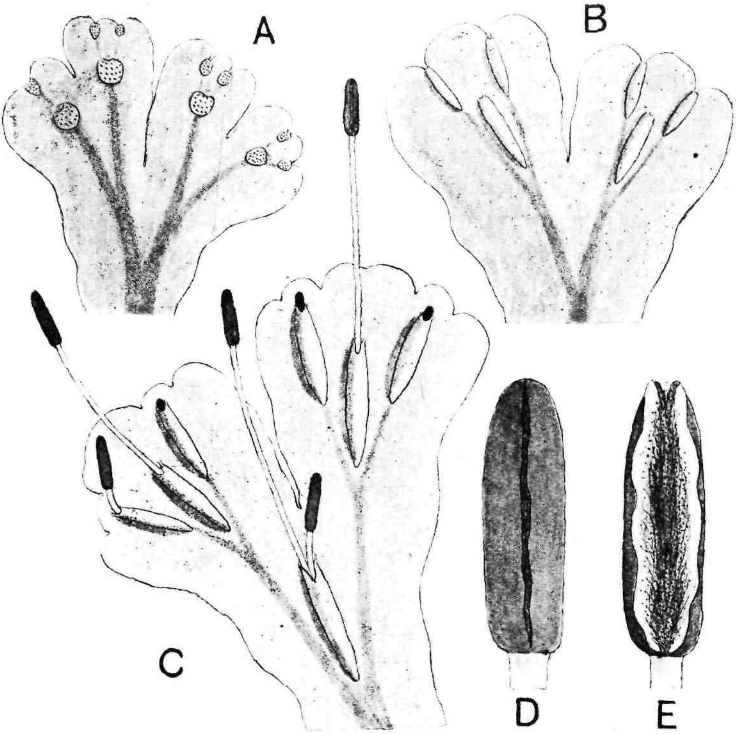
attributable to their very different habitats. *Targionia* is xerophilous, with well-developed thallus, assimilating filaments, and thick epidermis; *Cyathodium* grows in moist and shaded places and shows markedly hygrophilous characters. Lang investigated *C. foetidissimum* (the largest and least reduced species, with well-defined air-chambers and with tuberculate as well as smooth-walled rhizoids) and *C. cavernarum* (the most reduced species, with less regular air-chambers, no distinct midrib, inconspicuous ventral scales, and no thickened rhizoids). The thallus consists for the greater part of a single basal layer of cells, upon which are borne the air-chambers. The latter contain no filaments, and the thin-walled epidermal cells have strongly convex upper and lower walls, probably serving as lenses to collect the feeble light in which the plant lives. The male branches and the archegonial receptacles have much the same structure as in *Targionia*. The capsule has a well-developed apical cap, and the seta consists of only two or four rows of cells. For details, reference should be made to Lang's extremely interesting paper (13).

MONOCLEACEÆ.

The genus *Monoclea*, of which two species are distinguished by systematists (*M. Forsteri* in New Zealand, *M. Gottschei* in tropical and South America), is one of the most interesting among the Hepaticæ. The genus was founded by Hooker (11) for a plant discovered by Forster during Captain Cook's famous voyage and named by Forster "Anthoceros univalvis." Hooker showed that the plant was no *Anthoceros*, since its oblong capsule has no columella and opens by a single slit, giving it a spoon-like appearance. Gottsche (9) described the minute structure of the thallus, noting the presence of two kinds of rhizoids (some wide and thin-walled, others narrow and thick-walled) and the occurrence of fungal hyphæ in the lower tissue, the structure of the ripe sporogonium, the one-layered capsule-wall, and the long spirally thickened elaters. Later, Gottsche (10) discovered the oval cushion-like male receptacle in plants from Mexico. Leitgeb[1] noted that the thick-walled rhizoids are distributed over the whole underside of the thallus and lie parallel with it, while the thin-walled ones arise only from the thicker middle portion of the thallus and stand out at right angles to it. He concluded that *Monoclea* is more closely related to *Pellia* than to any of the Marchantiaceæ, though it

[1] Unters., III., p. 62; VI., p. 130.

resembles the latter in the possession of a cushion-like male receptacle, which he likened to that of *Fegatella*. Schiffner, who had evidently overlooked the later papers of both Gottsche and Leitgeb (since he says the male plant is unknown), places the genus in the Anacrogynous Jungermanniales, beside *Pallavicinia* and *Symphyogyna*. Ruge (17) found that in the development of the antheridium several transverse walls appear before any longitudinal

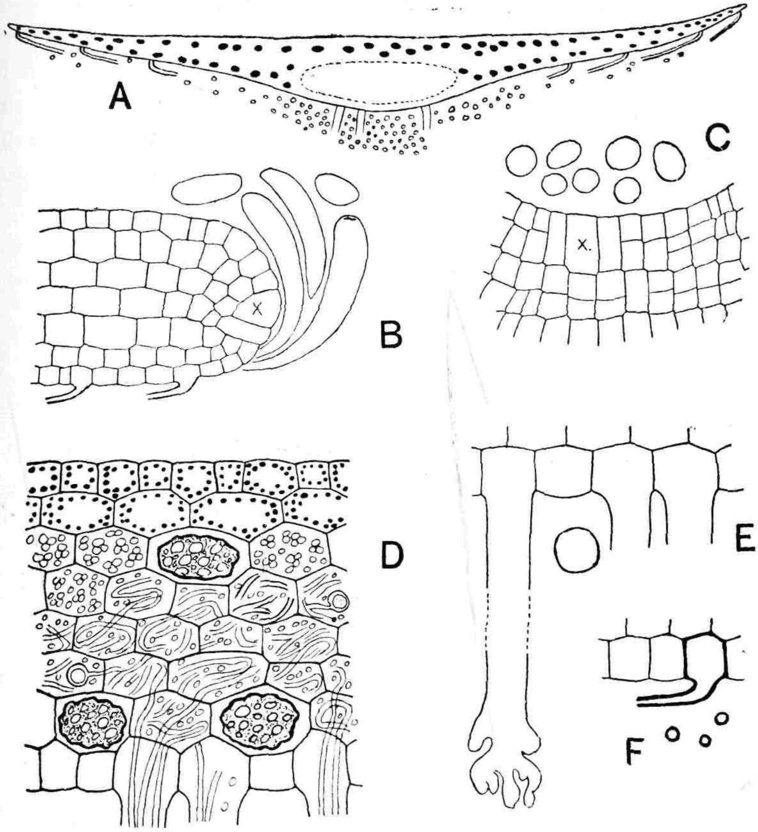


Monoclea Forsteri.

Fig. 14. A., Male plant, × 1. B., Female plant, × 1. C., Female plant, in which three capsules are exserted, × 1. D., Ripe capsule, showing dehiscence by a single longitudinal slit, × 4. E., The same, later; the margins have rolled back, exposing the mass of spores and elaters; × 4.

ones appear. Campbell (2), reviewing the work of the writers above-mentioned, concluded, from the presence of two types of rhizoids, the development of the male receptacle and the antheridium, and his own observation that the archegonium neck has six rows of cells, that *Monoclea* should be transferred to the Marchantiales and placed near *Targionia*. The writer (3, 4), from his examination of

abundant fresh New Zealand material, was able to add various



Monoclea Forsteri.

Fig. 15. A.—Transverse section of thallus. The large dots indicate the oil-bodies, the dotted line the position of the mycorhiza. The narrow rhizoids are shown mostly in cross section, the wide ones (of which three are shown) are only borne on the median portion of the thallus. ×15. B.—Vertical longitudinal section through the growing-point of the thallus, showing the apical cell (x) and the large club shaped mucilage-hairs; on the lower surface behind the apical cell are shown two of the narrow rhizoids. ×120. C.—Horizontal section through the growing-point, showing the apical cell (x) and its segments, with the large mucilage-hairs in cross-section. ×120. D.—Part of A., traversing the mycorhizal zone, the cells of which contain branching fungal hyphæ, some of the latter being shown in the rhizoids. Three of the oil-containing cells are shown; the cells above the mycorhiza contain starch-grains, and the two upper layers of cells contain chloroplasts. ×120. E.—Part of a vertical section of the thallus, showing three of the wide thin-walled rhizoids; on the left the branched free end of a rhizoid is shown. ×120. F.—Part of a section showing one of the narrow thick-walled rhizoids in longitudinal section, and three others in cross section. ×120.

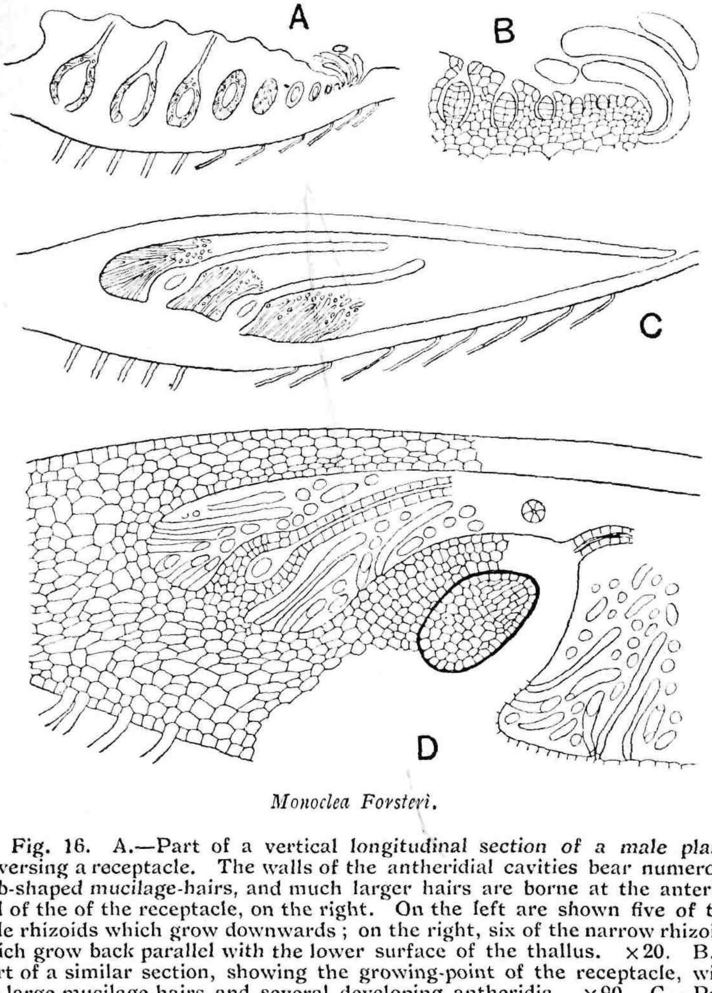
details, including the occurrence of large oil-bodies filling certain

cells of the thallus, the presence of a row of initial cells at the growing-point, and the formation of an octant-stage in the embryogeny—all of which are characteristic of the Marchantiales as distinguished from the Jungermanniales; the male receptacle was shown to differ from that of *Fegatella* (which it superficially resembles) by having a single anterior growing-point, as in the lower Marchantiales. A little later appeared a detailed paper by Johnson (12) on material collected in Jamaica, in which it was shown that the narrow rhizoids have the tubercles characteristic of the corresponding rhizoids of Marchantiales.

The thallus (Fig. 14) has a perfectly smooth upper surface, and there are no traces of air-chambers; while the only appendages on the lower side, in addition to the rhizoids, are the long club-shaped hairs which bend up over the growing-point (Fig. 15). The absence of chambers and of ventral scales, and the feeble development of tubercles in the narrow rhizoids, may be correlated with the extremely hygrophilous habitat of the plant. Coker (6) has shown that plants of *Dumortiera hirsuta* (allied to *Marchantia*) growing on porous sandy soil had well-developed air-chambers, while other plants that were constantly wet with dripping water had no trace of chambers. In *Dumortiera irrigua*, chambers are formed at the apex of the thallus, but soon become disorganised and are represented in the older parts only by the remains of the vertical walls, which form a network. Campbell (1) found that in *D. trichocephala* no trace of chambers can be detected even at the apex of the thallus. Hence in this hygrophilous genus we find every stage in the reduction of the chambers, related to the conditions of the habitat. Even in *Marchantia* itself, submerged plants or branches show a similar reduction of the chambers; and in *Fegatella* the writer (5) found that the submerged form had greatly reduced ventral scales and hardly a trace of tubercles in the rhizoids borne in the axils of the scales.

The only objections that can be urged against placing *Monoclea* in the Marchantiales are found in the position of the archegonia and in the form of the mature sporogonium. The archegonia are developed in a pit (Fig. 16) which becomes drawn out to form a long tube, much as in *Pellia*. However, the development of the tubular involucre of *Monoclea* is not in reality widely different from that of the hood-like involucre of the Corsiniaceæ or the two-lobed involucre of the Targioniaceæ. In these plants, as in *Monolcea*, the archegonia are produced on an unspecialised portion of the thallus,

and the form of the involucre depends merely upon the amount of the surrounding tissue which grows out and the rate at which it grows forward over or around the group of archegonia. Thus there is no real difficulty in homologising the involucre of *Monoclea* with

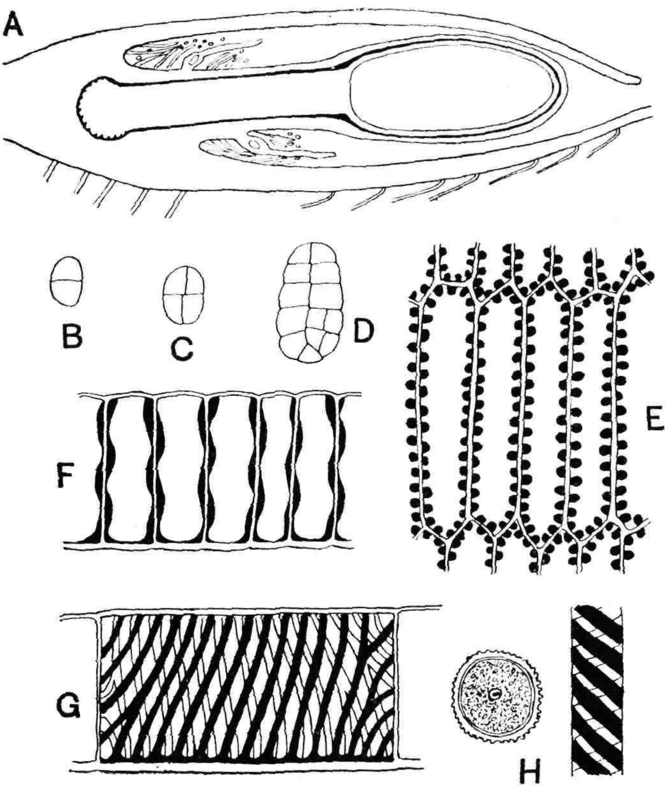


Monoclea Forsteri.

Fig. 16. A.—Part of a vertical longitudinal section of a male plant, traversing a receptacle. The walls of the antheridial cavities bear numerous club-shaped mucilage-hairs, and much larger hairs are borne at the anterior end of the of the receptacle, on the right. On the left are shown five of the wide rhizoids which grow downwards; on the right, six of the narrow rhizoids which grow back parallel with the lower surface of the thallus. ×20. B.—Part of a similar section, showing the growing-point of the receptacle, with the large mucilage-hairs and several developing antheridia. ×90. C.—Part of a vertical longitudinal section of a female plant, traversing a receptacle. Between the archegonia arise numerous long mucilage-hairs; rhizoids as in A. ×35. D.—Part of a similar section, showing a fertilised archegonium containing an embryo, and on the left of this an unfertilised archegonium. ×90.

that of the Corsiniaceæ and Targioniaceæ. The three families stand apart from the Ricciaceæ on one hand and the Marchantiaceæ on the other with regard to the arrangements for the protection of

the archegonia and the developing sporogonia. In Ricciaceæ each archegonium is simply sunk in a cavity of the thallus; in the Marchantiaceæ they are carried up on stalked archegoniophores, besides being protected, singly or in groups, by involucres; while in



Monoclea Forsteri.

Fig. 17. A.—Longitudinal section through a receptacle containing a half-ripe sporogonium, covered by the calyptra, on the sides of which, towards the base, are borne the unfertilised archegonia and some of the mucilage-hairs. ×35. B., C., D.—Young sporogonia in longitudinal section. ×90. E.—Part of the capsule-wall in surface view (outer surface), showing the ends of the fibrous thickenings on the vertical walls of the cells. ×200. F.—Part of the capsule-wall in transverse section. ×200. G.—A cell of the capsule-wall, rom a longitudinal section of the capsule, showing the two sets of fibres crossing each other on the cell-wall. ×200. H.—Spore in section and part of an elater in surface view. ×700.

the three intermediate families they are developed in groups on the free surface of the thallus and are protected by the hood-like outgrowth of the surrounding tissue.

It must be admitted that the habit of the sporogonium, with its long seta and its erect cylindrical capsule, differs greatly from that of any of the other Marchantiales. Apart from the embryology, which is of the Marchantia-type, *Monoclea* agrees with all known Marchantiales and differs from all Jungermanniales (except the Calobryaceæ) in that the capsule-wall is a single layer of cells in thickness (Fig. 17). Moreover, the great length of the seta may perhaps be related to the extremely hygrophilous habitat, enabling the capsule to be raised well above the wet substratum for the dispersal of the spores. In the Marchantiaceæ, where the sporogonia are raised well above the thallus by the stalked archegoniophore, there is no necessity for a long seta, and accordingly the latter simply elongates sufficiently to thrust the ripe capsule through the calyptra. It would appear reasonable to suppose that *Monoclea* represents a blindly-ending line of development arising from forms like the Corsiniaceæ or the Targioniaceæ—a line in which the sporogonium itself has assumed the function of thrusting the capsule upwards. In the main line of the Marchantiales, which leads from these lower forms to the Marchantiaceæ, this function has devolved upon the outgrowth (archegoniophore) of the thallus which carries up the group of fertilised archegonia.

LITERATURE OF RICCIACEÆ, CORSINIACEÆ, TARGIONIACEÆ, MONOCLEACEÆ.

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MARCHANTIACEÆ.

THIS order (the "Marchantiaceæ-Marchantioideæ" of Schiffner) is distinguished from all the lower groups of the Marchantiales by having stalked carpocephala. The thallus has (except in *Dumortiera*) well-developed air chambers, which are either arranged in a single layer or are divided up by partitions so as to form several superposed series as seen in transverse section. When in a single layer the chambers contain assimilating filaments (except in the Astroporæ). The pores on the thallus are either simple and surrounded by a single ring of cells or by several concentric rings, or are barrel-shaped. There are usually well-developed air chambers on the male and female receptacles, and these usually have the barrel type of pore. The antheridia are generally collected into a sharply defined cushion-like receptacle, which in the highest forms represents a branch-system, having several growing-points, and is then (except in *Fegatella*) stalked. The sporogonium is separable into foot, seta, and capsule; well-developed elaters are always present; the capsule opens by the separation of a more or less definite lid, or by splitting into several valves, or by both processes.

The organisation of the carpocephalum, or archegoniophore, varies a good deal in the different members of the order. In the highest forms (Leitgeb's "Compositæ") there are two or more groups of archegonia, developed in centrifugal succession by as many radially arranged branches or growing apices. Owing to the more rapid growth of the upper tissue of the convex receptacle, the archegonia are carried on to the lower surface, and the youngest archegonia then stand nearest the stalk. The succession of the archegonia is, of course, acropetal with reference to each of the archegonium-producing growing-points and centrifugal with reference

to the dorsal side of the receptacle itself—not centripetal, as is often erroneously stated. In the disk-like male receptacle of *Marchantia* and *Preissia*, the antheridia do not undergo this inversion, and the radiating centrifugal arrangement of these organs is at once evident.

In his "Compositæ," Leitgeb placed the genera *Lunularia*, *Dumortiera*, *Preissia*, *Marchantia*, and (doubtfully) *Fegatella*. The remaining genera of Marchantiales with stalked carpocephala which were known to him were divided into two groups which he named "Astroporæ" (*Clevea*, *Sauteria*, *Peltolepis*) and "Operculatæ" (*Plagiochasma*, *Reboulia*, *Grimaldia*, *Neesiella*, *Fimbriaria*). In these two groups, and also in *Fegatella*, the female receptacle was believed by Leitgeb to be in all cases merely a dorsal outgrowth of the thallus, the archegonia being developed singly on the periphery of the receptacle and each archegonium becoming enveloped by its own involucre; except in *Clevea* and *Plagiochasma*, however, the stalk of the receptacle has either a single furrow or two furrows, and this was taken by Leitgeb to indicate that the apex of the thallus entered into the formation of the stalk but not into that of the archegonium-producing region itself. The carpocephalum was therefore regarded as representing a single branch, the apex being used up in its development, whilst the "Composite" carpocephalum was interpreted as being composed of a branch system. Although the distinctions upon which Leitgeb founded this classification of the Marchantiaceæ can no longer be maintained, it will be convenient in this résumé to deal with the genera in three groups, corresponding with Leitgeb's "Astroporæ," "Operculatæ," and "Compositæ."

I.—Astroporæ.

Leitgeb named this group from the fact that the radial walls of the cells (arranged in a single ring) surrounding the thallus air-pores are as a rule strongly thickened, giving the pore a star-like appearance in surface view. Apart from the presence of exactly similar pores in other families (*e.g.*, in *Tessellina* and some species of *Plagiochasma*), there are several species of *Clevea* in which this thickening does not occur. However, there is no doubt that the three genera—to which a fourth (*Gollaniella*) has recently been added by Stephani (62) for a Himalayan plant allied to *Clevea*—form a natural group. Their geographical distribution, which presents some very interesting features, has been described by Solms-Laubach (59). The writer found representative species of all three genera (*Clevea hyalina*,

Sauteria alpina, *Peltolepis grandis*) growing, often intermingled, in several localities in the Bernese Oberland, and some additional details were made out in the structure and development of the sexual receptacles and of the sporogonia.

In this group the ventral scales are arranged in several series, as in *Corsinia*. The scales do not show the sharply marked apical appendages which are characteristic of the Operculatæ and Compositæ; in this respect the Astroporæ recall the Corsiniaceæ and Ricciaceæ. The air-chambers, which contain no assimilating filaments, are typically arranged in a single series, but in the median portion of the thallus they are divided up by secondary partitions. The capsule wall has well-developed fibrous thickenings in its cells; there is a small apical cap, and the capsule opens by irregular teeth.

In *Sauteria* and most species of *Clevea* the antheridial group is not sharply separated from the surrounding tissue, the antheridia being developed in long patches arranged in two irregular rows on the midrib; between the antheridial chambers, which have long ostioles, there are air-chambers, and the whole arrangement is hardly more definite than in various species of *Riccia*. In *Clevea Rousseliana* we get the first step towards the differentiation of a definite male receptacle, the group being shorter and the antheridial chambers more closely approximated to each other. In *Peltolepis* the antheridia are developed in definite rounded cushion-like receptacles, sharply marked off from the thallus and surrounded by a series of scales.

The chief interest of the group, however, lies in the organisation of the female receptacle (*Fig. 18*). In *Clevea* the receptacle arises as a dorsal outgrowth of the thallus tissue immediately behind the growing-point, which, after the young receptacle has been laid down, produces ordinary thallus tissue; and several receptacles may be formed in succession on the same branch of the thallus. The first archegonium is formed at the hinder end of the receptacle, and is followed by one at either side and finally one at the front. In the meantime the lower tissue of the receptacle has become a short stalk, which later lengthens out and carries up the receptacle with the sporogonia; while the archegonia, which at first stand vertically at the edge of the receptacle, are carried downwards owing to growth of the tissue above them, and at the same time each archegonium becomes enveloped by a sheath which grows out from the surrounding tissue. The curved necks of the archegonia at first project freely from the sheath (involucre) and are directed upwards. Scales grow out from the tissue below the archegonia,

and when the stalk lengthens these scales are carried up with the receptacle. The whole structure is apparently a mere dorsal outgrowth of the thallus tissue, the apical growth of the thallus not being arrested by the development of a receptacle. The receptacle of *Clevea* may therefore be compared with the outgrowth which

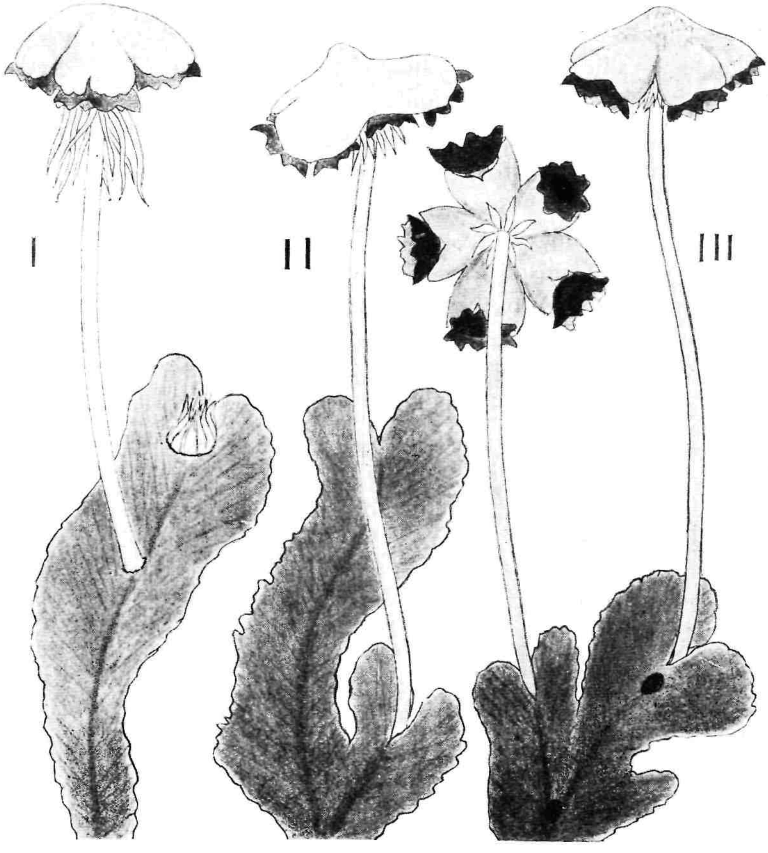

Fig. 18. *Astroporæ.*—I, *Clevea hyalina*; II, *Sauteria alpina*; III, *Peltolepis grandis.*

arises among the archegonia in *Corsinia*, but in *Clevea* the archegonia do not appear until the outgrowth has developed into a nearly hemispherical structure, about 0·1 mm. in diameter, and when the do appear they arise from the tissue of the outgrowth itself.

In *Sauteria* the receptacle begins in the same way as in *Clevea* but the apical growth of the thallus is arrested when a receptacle is formed, hence a branch of the thallus bears a single receptacle only. According to Leitgeb, a single archegonium is present in each involucre and a single groove in the stalk. The writer found,

however, several specimens of *S. alpina* with involucres each containing from two to four archegonia; in some cases two sporogonia had developed in an involucre, and frequently the stalk had two furrows containing the rhizoids, which spring from the underside of the receptacle between the involucres.

Apart from the constant occurrence of two rhizoid-furrows in the stalk, *Peltolepis* agrees closely with *Sauteria* in the structure of the carpocephalum. In *P. grandis*, which Leitgeb and other writers describe as resembling *Clevea* and *Sauteria* in having a single archegonium in each involucre, numerous cases were observed in the writer's Swiss specimens, in which each involucre had two, three, four, and even five archegonia in an involucre, though only one sporogonium was produced in the plants examined. Hence in both *Sauteria* and *Peltolepis* the carpocephalum is of the "Composite" type.

The Astroporæ form an interesting series, marked off from the other Marchantiaceæ by the structure of the thallus and by the scattered and simple ventral scales; while they are still more sharply distinguished from the Operculatæ by the structure of the capsule-wall.

II.—Operculatæ.

Leitgeb named this group from the mode of dehiscence of the capsule in the genera known to him. The capsule-wall has an apical lid which is either thrown off entire or breaks up irregularly, and the lower part of the dehisced capsule remains as an urn, usually with toothed margin. The cells forming the capsule-wall are devoid of special fibrous thickenings, though in the upper half of the capsule the cells often have their radial walls slightly thickened at the corners. From the Astroporæ the group is further distinguished by several other characters: the ventral scales are in two rows and have well-defined apical appendages (sometimes two or three to each scale); the pores on the thallus are surrounded by several concentric rings of cells; the pores on the sexual receptacles are barrel-shaped. It is more difficult to separate the Operculatæ from the Compositæ, for in all the genera, except *Plagiochasma* and and the incompletely known new genus *Massalongoa*, more than one archegonium may be developed in each involucre of the carpocephalum, and among the Compositæ there are genera which resemble the Operculatæ in thallus structure (*Bucegia*) and in the absence of fibres from the capsule-wall (*Lunularia*). Still, the group may be regarded as forming an independent series, showing

some striking parallelisms with the Astroporæ on one hand and the Compositæ on the other. In the structure of the carpocephalum

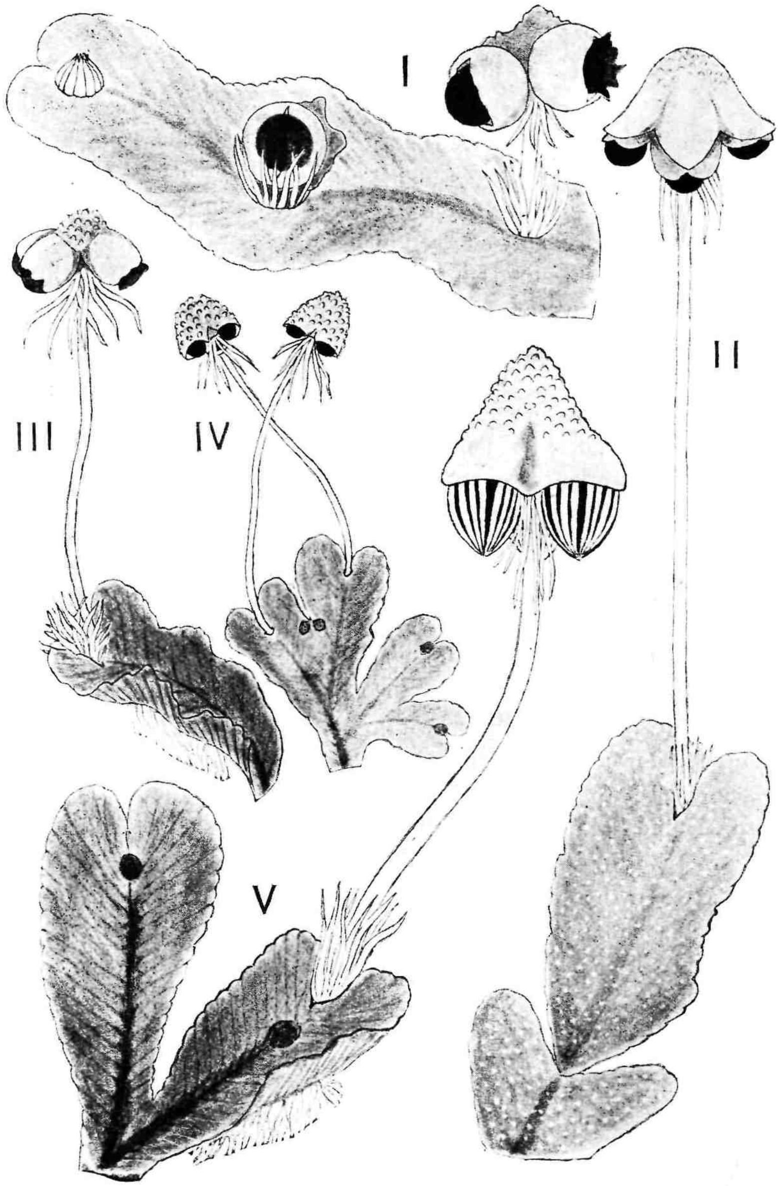

Fig. 19. *Operculatæ.* —I, *Plagiochasma rupestris*, female plant with three carpocephala; II, *Reboulia hemispherica*, with a carpocephalum; III, *Grimaldia fragrans*; IV, *Neesiella rupestris*, with two carpocephala and four male receptacles; V, *Fimbriaria Lindenbergiana*, with a carpocephalum and two male receptacles.

the genus *Plagiochasma* corresponds to *Clevea*, *Reboulia* to *Sauteria*, while the highest forms show a distinct approach to the Compositæ.

The air-chambers of the thallus are usually divided up by secondary partitions and plates, so that the whole upper region appears in section as a spongy mass of green tissue (Fig. 20). In some cases, however, the chambers are in a single layer and are then either empty (*Grimaldia pilosa*, *Neesiella*) or contain assimilating filaments (some species of *Grimaldia* and of *Fimbriaria*).

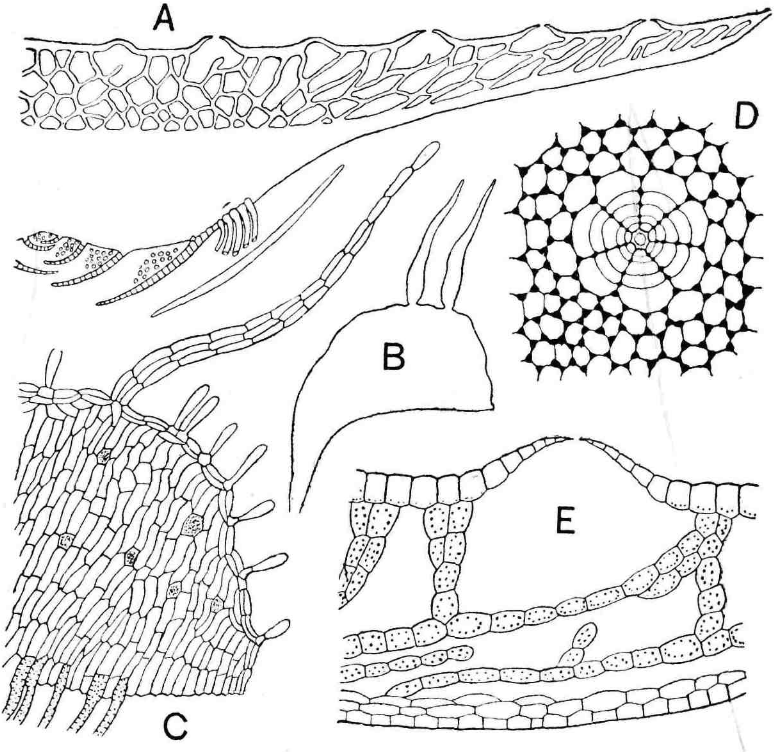

Fig. 20. *Reboulia hemispherica*. A.—Part of a transverse section of the thallus, showing the dorsal zone of green air-chamber tissue and the ventral zone of compact colourless tissue. On the midrib are shown the ventral scales in section, the small tuberculate rhizoids, and the large smooth-walled rhizoids. ×35. B.—A ventral scale, showing two long narrow appendages. ×35. C.—Part of a scale, showing one of the appendages, several marginal mucilage-hairs, some of the oil-cells (shaded), and some tuberculate rhizoids springing from the base of the scale. ×150. D.—Part of the dorsal epidermis in surface view from above, showing a pore surrounded by six concentric rings of cells, the walls of which, as in the rest of the epidermis, show angular thickenings. ×150. E.—Part of A., showing the structure of the lateral region (lamina) of the thallus; the compact ventral tissue is here reduced to two or three layers of cells. ×150.

The male receptacles are marked off from the surrounding tissue by a groove, from which arise scales that cover the receptacle

when young. The receptacle is rounded or oval, with a single anterior growing-point which produces the antheridia in acropetal succession; sometimes the apex branches during the development of the antheridia, so that the receptacle is forked in front (Fig. 21, c).

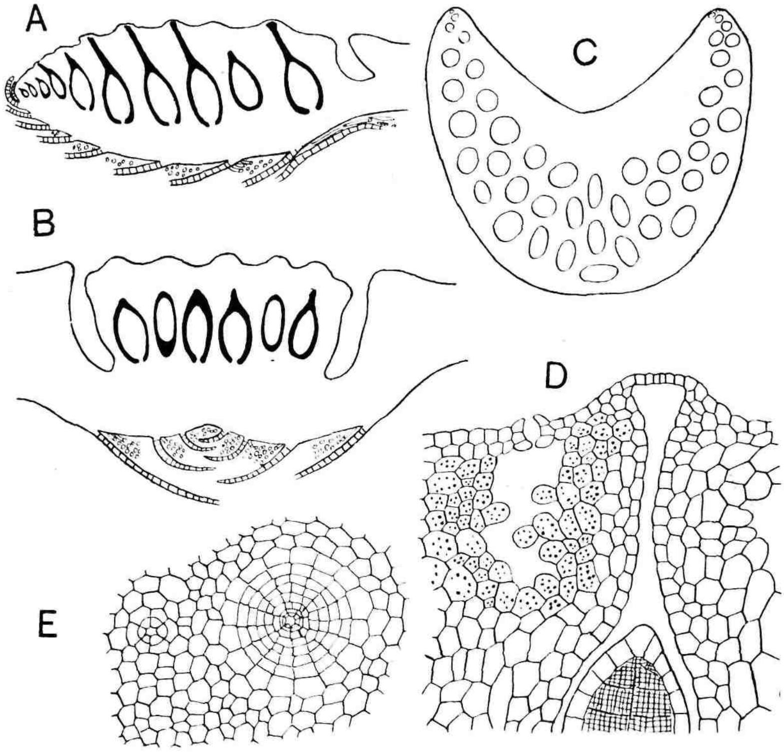

Fig. 21. *Reboulia hemispherica.* A.—Longitudinal section of male receptacle the antheridial cavities are shaded, and the scales and rhizoids on the ventral surface are shown in part. ×20. B.—Transverse section of male receptacle. ×20. C.—Horizontal section of a receptacle with two growing-points, the latter showing the youngest antheridia, whilst the oldest occupy the posterior part of the receptacle. ×20. D.—Part of A, ×150, showing on the right the upper portion of an antheridium and its cavity, on the left an air-chamber opening by a small barrel shaped pore; the cells around the air-chamber contain chloroplasts.

The growing-point may proceed to form ordinary tissue again, leaving the receptacle behind, and several receptacles may be produced one after another; or a female receptacle may be formed immediately in front of the male receptacle; or the apical growth may cease after the development of a male receptacle so that the latter stands at the margin of the thallus.

Plagiochasma (Fig. 19, I.), which stands at the base of this group, strikingly resembles *Clevea* (and differs from all the remaining Operculates) in the development of the carpocephala. The latter

are purely dorsal outgrowths, formed one after another; the stalk has no furrow; the central dorsal tissue of the receptacle is poorly developed; hence the bulk of the receptacle is made up of the involucres, each with a single archegonium. In addition to this detailed agreement in the carpocephalum, *Plagiochasma* further resembles *Clevea* in having usually a single ring of cells around each pore on the thallus, and in these cells radial thickening characteristic

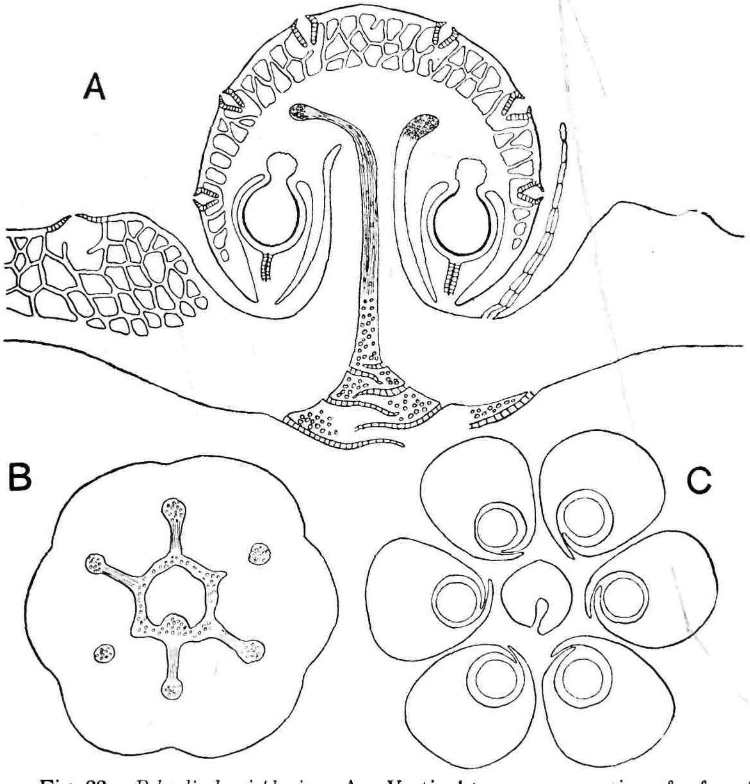

Fig. 22. *Reboulia hemisphærica.* A.—Vertical transverse section of a female receptacle and the adjacent portions of the thallus. Two developing sporogonia are shown, each enclosed in its calyptra. The outer portion of the receptacle shows air-chambers with barrel-shaped pores, the inner portion consists of compact starch-bearing tissue, and the groove of the receptacle stalk shows in its upper portion numerous tuberculate rhizoids, in its lower portion a number of ventral scales. On the right, one of the band-like scales is shown arising from the tissue at the base of the stalk. ×20. B and C.—Two horizontal sections of a female receptacle. ×20. A is from the upper portion of the receptacle and shows the six cavities from which spring tuberculate rhizoids, the latter passing into the groove on the ventral surface of the stalk. B is taken at a lower level and shows six sporogonia in outline, each in its involucre.

of the Astroporæ. Four archegonia are usually formed, but frequently only two or three sporogonia, or even a single sporogonium may come to maturity. The upper portion of the capsule-wall

consists of two to our layers of cells, forming a cap which breaks into fragments when dehiscence occurs. The young carpocephalum is protected by two rings of scales; when the stalk elongates the inner scales are carried up on the receptacle, while the outer scales remain at the base of the stalk.

In all the other genera of Operculatæ, the carpocephalum stalk has a rhizoid groove, and the development of a carpocephalum terminates the growth of the thallus.

In *Reboulia* (Figs. 19-23), which is the only genus represented in

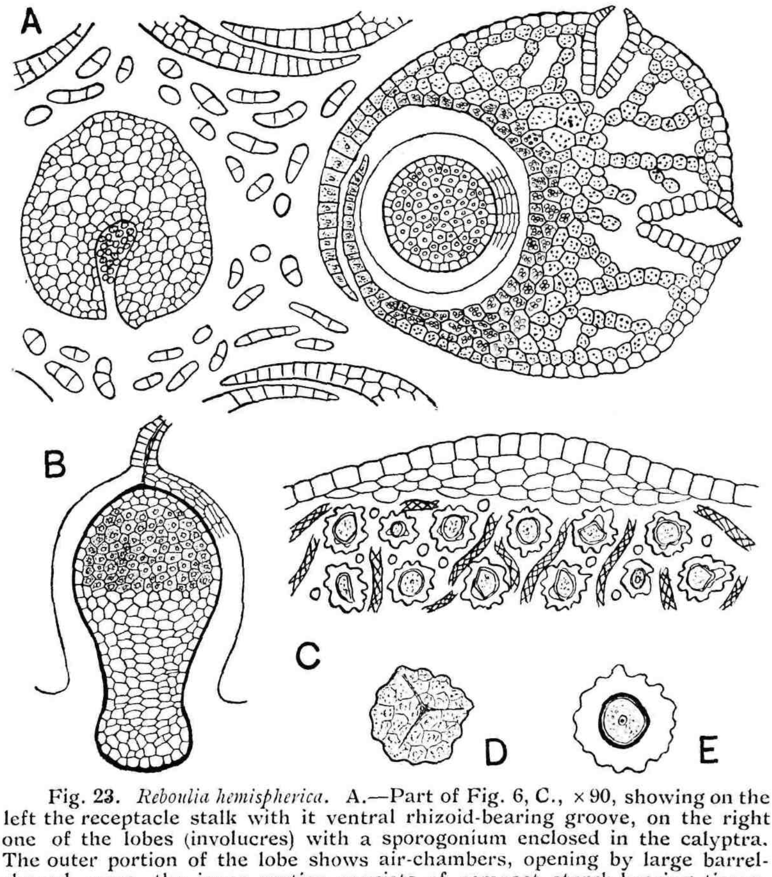

Fig. 23. *Reboulia hemispherica.* A.—Part of Fig. 6, C., × 90, showing on the left the receptacle stalk with it ventral rhizoid-bearing groove, on the right one of the lobes (involucres) with a sporogonium enclosed in the calyptra. The outer portion of the lobe shows air-chambers, opening by large barrel-shaped pores, the inner portion consists of compact starch-bearing tissue. Between the stalk and the involucre are shown the narrow scales in cross-section. B.—Longitudinal section of a young sporogonium, with its calyptra. In the upper portion (capsule) of the sporogonium the archesporial tissue is shaded. × 90. C.—Upper portion of a nearly ripe capsule in longitudinal section, showing the lens-shaped apical cap and some of the spores and elaters. × 120. D.—Spore in surface view, from the inner side, showing the three radiating ridges. The surface is covered with a network of smaller ridges. × 200. E.—Spore in section, showing the thin endospore, the exospore (shaded), and the thick outer coat (episporc) with its ridges. × 200.

Britain, the carpocephalum, which has well-developed air-chambers, is conical or hemispherical when young, with four to seven thick lobes, the margins of which form bivalved involucres, each with a single archegonium (sometimes two archegonia). When the capsules ripen, the lobes spread upwards and outwards, so that the receptacle becomes nearly horizontal. The apical portion of the capsule-wall, which has a well-developed cap (Fig. 23), falls away in fragments when the capsule opens. The series of figures given here will serve to illustrate the structure of this plant, which forms a good average type of the Operculatæ.

Grimaldia (Fig. 19, III.) and *Neesiella* (Fig. 19, IV.) are closely allied to *Reboulia*, but the upper portion of the capsule-wall becomes detached in a single piece, forming a well-defined lid. The limit of the latter, and the dehiscence of the capsule, are in these two genera determined by an annulus consisting of small cells, which does not occur in any of the other Operculatæ. Moreover, in these genera the sinuses from which spring the rhizoids that run into the furrow of the carpocephalum stalk bulge slightly outwards and are visible as short lobes on the outer surface of the carpocephalum, alternating with the bell-shaped involucres; these lobes correspond with the long hollow rays seen in *Marchantia*. In both genera, also, the writer has found that the involucres frequently contain two (*Grimaldia fragans*, *G. dichotoma*) or as many as four (*Neesiella rupestris*) archegonia. The archegonia have usually been described as occurring singly in the involucres, though Leitgeb noted the occurrence of two archegonia in one case in *Neesiella*. In one specimen of *Grimaldia fragans* the writer found two sporogonia in an involucre, but in several cases every involucre examined had two archegonia.

In *Cryptomitrium*, Abrams (1) has shown that each involucre contains a group of archegonia (usually five) which show centrifugal development exactly as in the Compositæ. Moreover, Stephani (61) states that the stalk often has two furrows, and we have here again a typical "Composite" carpocephalum, with five or six growing-points from which the archegonia are developed.

The large genus *Fimbriaria* differs from the other Operculatæ in having a special envelope (perianth) around each archegonium, arising from the tissue inside the involucre; in this respect the genus resembles the highest types of the Marchantiaceæ (*Preissia* and *Marchantia*). The recently discovered Himalayan genus *Massalongoa* is said by Stephani (62) to stand near *Fimbriaria*, but it has no perianth. The perianth of *Fimbriaria* is a striking and beautiful

structure (Fig. 19, V.), giving the fruiting carpocephalum a very characteristic appearance, since it protrudes beyond the involucre and its margin is cut up into from four to sixteen long narrow segments, which in some species remain attached at the tips and serve to bring about the gradual dispersal of the spores by acting as a "censer mechanism." Campbell (8) has shown that in *F. californica* the carpocephalum is "Composite," as in *Cryptomitrium*, each of the four involucres containing a group of four archegonia as a rule. In *F. Lindenbergiana*, several receptacles were found by the writer to contain two, three, or four archegonia in some of the involucres, and probably the same will be found in other species of this genus.

III.—Compositæ.

This group contains eight genera—*Exormotheca*, *Fegatella*, *Lunularia*, *Wiesnerella*, *Dumortiera*, *Bucegia*, *Preissia*, and *Marchantia*, all poor in species except *Marchantia*.

The air-chambers are arranged in a single layer, except in *Bucegia* where they are partitioned up as in *Reboulia* and the other typical Operculatæ. There are usually assimilating filaments filling up the chambers, but exceptions occur (apart from *Bucegia*) in the genus *Dumortiera*, in which the air-chamber layer shows great reduction. The extent of the reduction varies in different species, and in the same species according to the conditions of the habitat with reference to moisture and shade. In *D. hirsuta* (in which *D. irrigua* is merged by Stephani) the air-chambers are laid down at the growing-point and, as shown by Coker (17), in plants grown under fairly dry conditions may persist and be roofed over, but in conditions of shade and moisture (in which the plant usually grows) the chambers become disorganised and are only recognisable in the parts behind the apex by the remains of the vertical partitions. In *D. velutina*, the partition-walls and the roofing layer soon become completely disorganised, but the thallus is densely clad with outgrowths corresponding to the assimilating filaments which fill the chambers in other genera. In *D. trichocephala*, according to Campbell (8), there is no trace whatever of the chambers even at the growing-point, but Ernst (20) and Kamerling (29) found that the assimilating filaments are represented by short projecting papillæ. In *Bucegia*, *Preissia*, and *Marchantia*, the thallus pores are barrel-shaped, but in the other genera (as in the Operculatæ) this type of pore is confined to the sexual receptacles, the pores on the

thallus being surrounded by concentric rings of cells. In *Exormotheca* the roof of each chamber grows up to form a long chimney-like projection with the pore on its summit; this is merely an exaggeration of the convex form of roof seen in *Fegatella* (Figs. 24, 25).

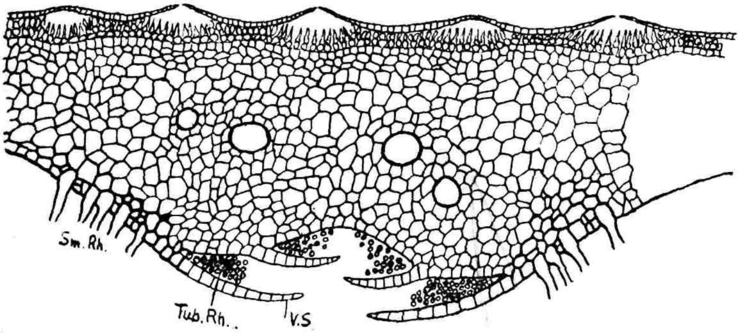

Fig. 24. *Fegatella conica.* Transverse section through midrib of thallus showing the upper zone of air-chambers and the lower zone of compact tissue, with four of the mucilage sacs. Sm. rh., smooth-walled rhizoids; tub. rh., tuberculate rhizoids; v.s., ventral scales. × 30.

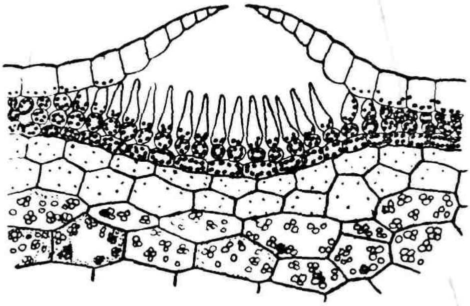

Fig. 25. *Fegatella conica.* Part of a vertical section of the thallus, showing an air-chamber, lined by pointed cells and opening above by a pore in the epidermis. × 180.

In this group the Marchantiaceous thallus reaches its greatest complexity. The compact tissue underlying the air-chamber layer contains large oil-bodies, filling up certain cells; mucilage sacs, either isolated, or arranged in groups (*Exormotheca*), or in longitudinal rows (*Fegatella*); sclerotic fibres (*Preissia*—Fig. 27—and some species of *Marchantia*); and a mycorhiza (*Preissia, Fegatella*). The ventral scales are generally well developed (except in *Dumortiera*, where they are rudimentary, as might be expected from the hygrophilous habitat), and have an apical appendage separated from the

rest of the scale by a deep constriction; the appendages of the younger scales curl upwards over the growing-point (Fig. 26).

The male receptacles are sessile in the lower genera. The simplest type is seen in *Exormotheca*, where the antheridial chambers are developed in a zigzag row along the middle of the thallus. In *Lunularia* the receptacle has the same structure as in

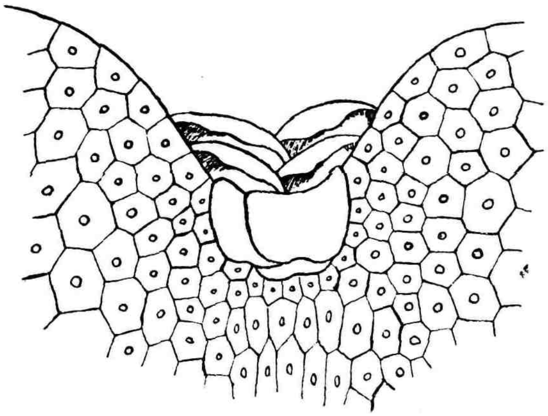

Fig. 26. *Fegatella conica*. Growing point from above, showing the reflexed scales and the areolation of the thallus. ×10.

Reboulia; the antheridia, which are developed in acropetal succession, are peculiar among Marchantiales in having a long slender stalk. In *Wiesnerella*, *Fegatella*, and *Dumortiera*, the receptacle evidently represents a branch-system, since the antheridia are (especially in *Fegatella*) clearly arranged in several radiating rows. In *Bucegia*, *Preissia*, and *Marchantia*, the receptacles are definitely radial and lobed (palmate in some species of *Marchantia*), with a zigzag row of acropetally developed antheridia to each lobe, and the receptacle is raised above the thallus on a stalk with two furrows; here the receptacle is undoubtedly a branch-system, having as many growing-points as there are lobes.

The carpocephala vary considerably in structure, but in all cases they are terminal on the thallus and each involucre contains a group of archegonia, except in *Fegatella* where there is but one archegonium as a rule. The simplest carpocephalum is that of *Exormotheca*, which has two involucres, standing right and left; the central tissue above and between the involucres is little developed, as in *Clevea* and *Plagiochasma*, but the stalk has a furrow and the involucres contain several archegonia. *Lunularia* is exceptional in that the carpocephalum stalk has no furrow, but in

the remaining genera there are two furrows. In *Wiesnerella*, with six to eight involucres, and in *Dumortiera*, with as many as sixteen,

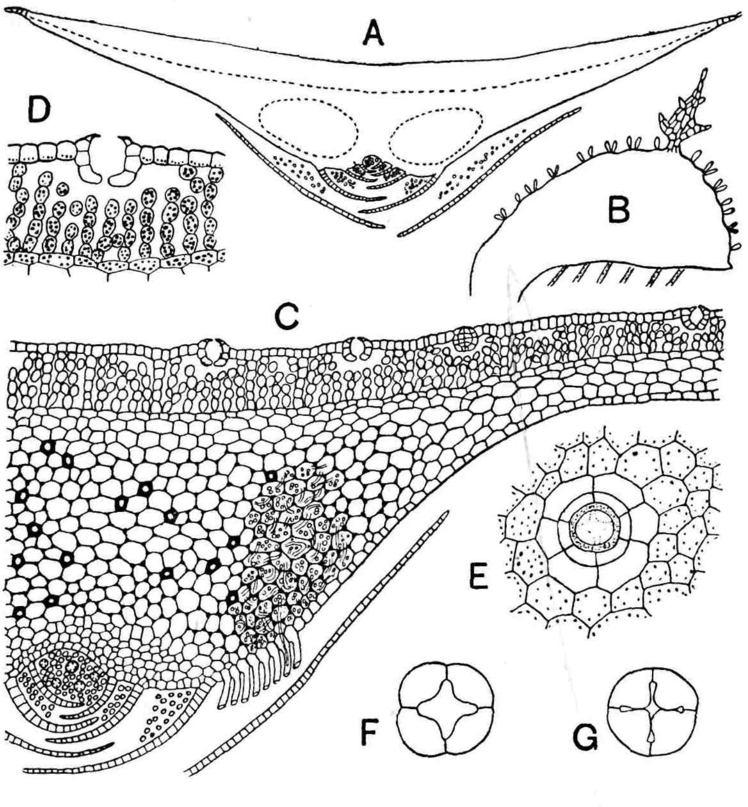

Fig. 27. *Preissia commutata*. A.—Transverse section of thallus. The two areas enclosed by dotted lines indicate the position of the mycorhiza, and the depth of the air-chamber zone is shown by the upper dotted line extending across the thallus. At the margins there is a membrane one cell thick and four or five cells broad. × 20. B.—A ventral scale, showing its pointed appendage, the club-shaped mucilage hairs on the free margin, and some of the tuberculate rhizoids springing from the base of the scale. × 35. C.—Part of A., × 60, showing the upper zone of air-chambers and the lower zone of compact tissue. In the latter, part of the mycorhiza is shown with fungal hyphæ, and one of the latter is seen entering by a smooth-walled rhizoid on the side of the midrib. On the lower side are shown the overlapping scales and the bundles of tuberculate rhizoids. D.—Part of C., × 120, to show the structure of an air-chamber. The floor of the chamber consists of green cells, and from it arise branched green filaments. Chlorophyll is also present in the epidermal cells. E.—Part of the epidermis in surface view, from above, showing two rings of cells around the pore, with the thin membrane covered with resinous grains. The dotted lines indicate the position of the lowest ring of cells. × 200. E and F.—The lowest ring of cells in surface view, from below. In E the pore is open, in F it is almost completely closed. × 200.

the receptacle is like that of *Fegatella* in external appearance; but in *Preissia* and *Bucegia*, which have four involucres, the rhizoid-

bearing sinuses alternating with the involucres project outwards as ridges (Fig. 28, A and B).

The species of *Marchantia* differ a good deal in the organisation of the carpocephalum. The simplest type is seen in *M. geminata*.

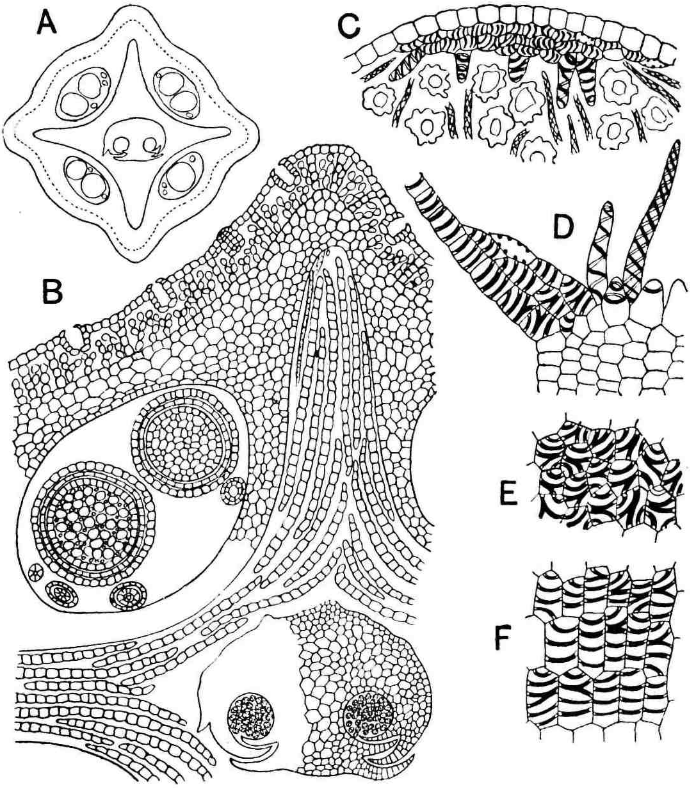

Fig. 28. *Preissia commutata*. A.—Horizontal section of a female receptacle, showing the four lobes and the alternate archegonial groups with young sporogonia and unfertilised archegonia. × 15. B.—Part of A, × 60, showing the receptacle-stalk with its two ventral rhizoid-grooves and one of the archegonial groups in which two sporogonia are developing. Beside the young sporogonia are shown four unfertilised archegonia. The outer tissue of the receptacle contains air-chambers, the inner tissue contains abundant starch-grains, and the hollow lobe is nearly filled with scales, seen in section. C.—Upper portion of a nearly ripe capsule in longitudinal section, showing the lens-shaped apical cap, the cells of which bear ring-like fibres and from which there project some fixed elater-like cells. × 90. D.—Lower portion of capsule in longitudinal section, showing the basal thickening of the capsule-wall and the fixed elaters occupying the bottom of the capsule. × 90. E and F.—Capsule-wall in surface view. E is from the upper, F from the lower portion of the capsule. × 90.

Here the carpocephalum has four spreading flat branches, each of which is notched at the free end and bears on its underside a group of archegonia surrounded by an involucre, the latter being formed

by the downward growth of the tissue of the branch and somewhat resembling the bilobed involucre of *Targionia*. In most species of *Marchantia*, however, there are, alternating with the involucres, hollow lobes from which spring the rhizoids that pass into the furrows of the stalk. In *M. polymorpha* these lobes grow out to form long hollow rays, of which there are generally nine—one in excess of the number of involucres. The same numerical relation is seen in other species of *Marchantia* with alternating involucres and lobes; the number of involucres varies from four to ten, and there is always one involucre short as compared with the number of lobes. However, the morphology of the carpocephalum will be discussed presently in considering the phylogeny of the Marchantiales

The capsule-wall has ring-fibres, except in *Lunularia* where their complete absence recalls the capsule structure of the Operculatæ. In *Fegatella*, *Lunularia*, and *Dumortiera* there is a well-developed apical thickening which is thrown off as a lid, the lower portion of the capsule then splitting into from four to eight teeth. In the other genera the apical cap is only indicated by an imperfect or loose layer of cells lying within the normally single-layered capsule-wall at the apex, and the capsule opens by teeth extending to the apex.

Phylogeny of the Marchantiales.

From our survey of the Marchantiales, it is evident that on the whole we can trace within this phylum, starting from *Riccia*, a general advance in the elaboration of the vegetative organs, the aggregation of the sexual organs into gametophores of increasingly complex organisation, and a progressive differentiation of the sporogonium.

The simplest thallus structure is that seen in most species of *Riccia*, where the upper tissue consists of filaments separated by narrow air-spaces. But within the genus *Riccia* itself we find the higher type of assimilating tissue which is characteristic of the Marchantiales as a whole—the widening of the spaces to form roofed-over chambers, with or without the partitioning up of the chambers so as to form a spongy mass of tissue. In the higher Marchantiales, practically the only further advances made in the elaboration of the air-chamber zone are the development of assimilating filaments by outgrowth of the cells forming the floor of the uniseriate chambers (*Corsinia*, *Boschia*, *Targionia*, some species of *Grimaldia* and *Fimbriaria*, all the Compositæ except *Bucegia*); and

the elaboration of the pores, which may remain surrounded by a single ring of cells with thickened radial walls, or may have several concentric rings of cells, or superposed tiers of cells forming a barrel-like structure. The elaboration of the thallus has clearly taken place independently in several distinct lines, and is only in a very general way correlated with the advance made by the members of each line in other respects.

Much the same may be said of the sporogonium. The early stages in differentiation are, to so speak, hurried through in the lower Marchantiales, and then the sporogonium makes practically no further advance. From the sterilisation of a single peripheral layer (*Riccia*) we pass to that of certain archesporial cells—serving at first for nutrition (*Corsinia*) and then acquiring the additional function of assisting in spore-dispersal by becoming thickened locally (*Boschia* shows the beginnings of this)—and to the differentiation of foot, seta, and capsule. The capsule-wall remains one cell thick, except for the apical cap found in Targioniaceæ and Marchantiaceæ, and (except in Ricciaceæ, *Corsinia*, the Operculatæ, and *Lunularia*) acquires fibrous thickenings. Except in a very general way, the sporogonium affords very little guidance to the phylogeny of the Marchantiales. Taken along with other characters, however, it helps in indicating the probable relationships of the groups.

The sexual receptacles, on the other hand, show a wide range of organisation, starting from *Riccia*, where the individual sexual organs are scattered over the median portion of the thallus, each antheridium and archegonium sunk in its own cavity, and leading to the complex stalked gametophores of *Marchantia*. The evolution of the male receptacle need not be traced in detail, but it may be noted that once the antheridia have been aggregated into receptacles and the latter have by a further step been sharply defined from the ordinary thallus tissue, the further advance of the male receptacle has, so to speak, lagged behind that of the female receptacle. Only in the highest members of the phylum does it become a definite branch-system with several growing-points, raised above the thallus on a grooved stalk. In the forms intermediate between these highly organised types and the Ricciaceæ, the male receptacle is at the most a mere ridge or cushion borne dorsally on the thallus or situated terminally on a branch whose growing-point is used up in the development of the receptacle.

It is not difficult, on biological grounds, to understand why the

female receptacle should have made more rapid advance in elaboration than has been the case with the male receptacle. The function of the antheridia is accomplished when they have matured and liberated the antherozoids; but the archegonia and the tissues surrounding them are concerned with the important and often prolonged processes of nourishing and protecting the developing sporogonia. Moreover, the working out of efficient methods for spore-dispersal has clearly played an important part in the evolution of the carpocephalum, and the first decided step in this direction would be the elevation of the sporogonia above the general surface of the thallus.

The starting point in the evolution of the carpocephalum is evidently to be found in the Corsiniaceæ, which are not very far removed from the Ricciaceæ. No known species of *Riccia* shows a definite archegonial group, but in *Tessellina* we get an approach to a female receptacle, for the archegonia are no longer sunk in the general thallus tissue. The envelope which grows up around each archegonium may be compared with the involucre of higher forms, and if the archegonia were developed in small groups and each group were raised above the thallus on a stalk formed by growth of the underlying tissue, we should have a carpocephalum comparable with that of *Clevea* or *Plagiochasma*. In the latter genera, however, the archegonia are not developed until the receptacle has arisen as an outgrowth behind the growing-point of the thallus, and they are developed upon this outgrowth, each archegonium becoming surrounded by an involucre. The gap between *Tessellina* on one hand and *Clevea* and *Plagiochasma* on the other is to a large extent bridged by *Corsinia*, where an outgrowth arises in the midst of the archegonial group in a depression of the thallus, the outgrowth appearing after the archegonia have begun to develop. In *Corsinia*, therefore, we have a primitive carpocephalum which arises at a late stage as compared with the carpocephalum of *Clevea* or *Plagiochasma*; its further development depends upon the fertilisation of the archegonia, and in any case it never becomes more than a scale which is thrust to one side during the development of the sporogonium, the latter being protected from the first by its own thick calyptra rather than by the incipient carpocephalum.

The affinities of the Targioniaceæ and of *Monoclea* have already been discussed, and we have seen that the involucre of these forms may be directly compared with the hood-like scale which arises behind the archegonial group of *Boschia*. *Cyathodium* has clearly

arisen by reduction, correlated with adaptation to a moist and shaded habitat, from a *Targionia*-like type, while the anomalous characters of *Monoclea* may also be explained as due to still more complete adaptation to a hygrophilous or almost aquatic mode of life. These three genera occupy a somewhat isolated position in the Marchantiales, and there is much to be said for the view that they represent an independent line derived from a *Boschia*-like type.

It is hardly an exaggeration to say that, beyond the possession of a stalked carpocephalum, the Marchantiaceæ are not distinguished from the four lower families of Marchantiales by a single character of importance. The Astroporæ form a fairly natural group, marked off from the Corsiniaceæ by the stalked carpocephalum and the well-developed elaters, and from the Operculatæ by the fibrous thickenings in the cells forming the capsule-wall. The Operculatæ and Compositæ, however, form much less natural divisions. The apical thickening of the capsule-wall and the dehiscence of the capsule by the throwing off of a lid are characters found in the Targioniaceæ and in practically every genus of Marchantiaceæ, though apparently it is only in the Operculate genera *Grimaldia* and *Neesiella* that the operculum is definitely delimited by an annulus of small cells. The structure of the thallus is remarkably uniform throughout the Operculatæ, and a second common character is the absence of fibres from the capsule wall, but in all the genera that have been investigated, except *Plagiochasma*, we find an approach to the definitely "Composite" type of carpocephalum. On the other hand, *Fegatella*, which we can hardly place elsewhere than in the Compositæ, resembles the typical Operculatæ in having as a rule a single archegonium in each involucre; while *Bucegia* and *Lunularia* show "Operculate" characters in the air-chamber layer and the capsule-wall respectively. It is hardly necessary to emphasize the contention that the organisation of the carpocephalum affords the best clue to the phylogeny of the Marchantiaceæ. For instance, *Marchantia* and *Lunularia* alone among Marchantiales possess gemmæ, and it is hardly likely, even in a group so rich in examples of homoplasy as the Hepaticæ, that precisely the same peculiar type of gemma should be evolved in widely separated types. Yet the two genera differ widely in apparently important characters; *Marchantia* has barrel-like thallus pores, a stalked male receptacle with several growing-points, a perianth around each archegonium, and ring-fibres in the capsule-wall, while *Lunularia* has simple thallus pores, a sessile male

receptacle with a single anterior growing-point, no perianth, and no ring-fibres.

The earliest stages in the development of the carpocephalum of the higher Marchantiales were first fully worked out by the writer for *Fegatella* (14) ; *Preissia* and *Marchantia* give similar results so far as these stages are concerned. When the formation of a carpocephalum is about to begin, the growing-point of the thallus broadens out and undergoes a first dichotomy, a "middle lobe" being formed between the two new growing-points exactly as in ordinary apical branching. Each of these growing-points becomes broadened and undergoes dichotomy. In *Preissia* branching stops at this stage, but in *Marchantia polymorpha* each of the four growing-points divides again, giving eight growing points; in both genera each of the growing-points eventually produced gives rise to a series of archegonia. In the case of *Fegatella* only two of the four growing points divide again, as a rule, and each of the six growing-points usually produces only one archegonium.

There is every reason for the belief that the carpocephala of all Marchantiaceæ, excepting *Clevea* and *Plagiochasma*, will be found to show the "Composite" mode of development just described, and that the organisation of the fully developed carpocephalum will be found to depend upon differences in detail in the later stages of growth. Thus, the presence in the stalk of a single furrow or of two furrows probably depends upon differences in (1) the rapidity with which the early apical divisions succeed each other and (2) the amount of growth which occurs in the tissue at the base of the developing carpocephalum. The fact that repeated dichotomy of the apex has been demonstrated in the development of the carpocephalum of *Fegatella*, despite the fact that the archegonia are usually produced singly in the involucres—that is, one archegonium from each growing-point—certainly suggests that the carpocephala of all the Marchantiaceæ, except *Clevea* and *Plagiochasma*, represent branch-systems, and that they differ only in such details as form, size, number of furrows in the stalk, presence or absence of projecting rhizoid-sinuses, presence or absence of perianths, number of archegonia produced by each growing-point.

Leitgeb distinguished three types of carpocephalum in the Marchantiaceæ: (1) the *Clevea* and *Plagiochasma* type, with furrowless stalk, and one archegonium in each involucre; (2) the Operculate type, including the Astroporæ, the Operculatæ, and *Fegatella*, with a single groove (two in *Peltolepis*) and a single archegonium in

each involucre; (3) the Composite type, with a two-furrowed stalk (except *Lunularia*) and several archegonia in each involucre. The first type of carpocephalum was regarded by Leitgeb as a purely dorsal outgrowth of the thallus; the second as representing a single branch, the growing-point of which is used up in the development of the carpocephalum without undergoing dichotomy; and the third as being composed of a branch-system, the growing-point being not only used up but undergoing repeated dichotomy during the formation of the carpocephalum, this dichotomy occurring at an early stage and affecting the whole carpocephalum and not merely the stalk. As we have seen, however, the facts recently discovered have broken down the distinction between Leitgeb's second and third types, and we are probably justified in regarding the carpocephalum which terminates the apical growth of the thallus as being in all cases formed by repeated dichotomy of the apex, resulting in from two to sixteen growing-points, each of which may produce either a single archegonium or a series of archegonia. In *Clevea* and *Plagiochasma* the carpocephalum when fully developed has much the same structure as in the other Marchantiaceæ which have a single archegonium in each involucre, except for the absence of rhizoids from the receptacle and of a groove from the stalk, and it can hardly be doubted that we have even here a difference in degree rather than in kind as compared with the carpocephalum of other genera. That is to say, the difference between the "dorsal outgrowth" carpocephalum of these two genera and the "branch system" carpocephalum of the other Marchantiaceæ depends upon the behaviour of the growing-point in the early stages of development.

Exormotheca presents what is perhaps the simplest type of a definitely "Composite" carpocephalum, which here consists of a branch system with two growing-points. The apex undergoes a single dichotomy, and each of the growing-points produces a series of archegonia, the latter being developed in centrifugal succession, in each series, with reference to the centre of the dorsal side of the receptacle. This Composite receptacle differs from the *Clevea* type chiefly in the hastening of the events that take place in the laying down of the young carpocephalum. The growing-point now enters into the composition of the receptacle from the very first, undergoing dichotomy and becoming used up in the development of the archegonia, so that the formation of a receptacle necessarily terminates the apical growth of the thallus on which it is borne. The presence of ventral scales and of rhizoids, the latter passing into the furrow

of the stalk, may obviously be regarded as confirming the interpretation of the Composite receptacle, found in all Marchantiaceæ except *Clevea* and *Plagiochasma*, as a branch system, which shows increasing complexity in the higher forms of the *Marchantia*-series. The development of a single archegonium in each involucre can no longer be taken as an indication that the carpocephalum differs in nature from the Composite type, but at the same time the interaffinities of the Marchantiaceæ are difficult to disentangle, and it is probable that the presence of a single archegonium in the involucre is (apart from the cases of *Clevea* and *Plagiochasma*) due simply to reduction and is not a primitive character.

As already pointed out, the evolution of the stalked carpocephalum is closely correlated with the facilitation of spore-dispersal, which has also been the chief factor in the evolution of the sporogonium. In the Ricciaceæ the spores can only escape by the decay of the surrounding thallus tissue in which the sporogonium is embedded (*Riccia*), or that of the envelope projecting above the general level of the thallus (*Tessellina*), in addition to the disorganisation of the thin capsule-wall and calyptra. *Tessellina* marks a great advance upon *Riccia*, in that the sporogonium is raised above, instead of being deeply sunk in, the thallus, and the spores no longer have to wait until the decay of the whole thallus sets them free. With this shifting of the sporogonium to the surface we may correlate its differentiation, first seen in *Corsinia*, into foot and capsule, and the sterilisation (already indicated in *Tesellina*) of some of the archesporial tissue of the capsule. The sterile archesporial cells have the primary function of supplying food to the developing sporogenous cells, and in *Corsinia* this is their sole function. In *Boschia*, however, the sterile cells lose their solid contents before the spores have ripened, and then (having acquired annular and spiral fibrous thickenings) serve for the conduction of water and salts to the developing spores, becoming elongated in order to perform this second function more efficiently. Finally, in the higher Marchantiales the elaters become greatly elongated and assume a third function after the dehiscence of the capsule, namely that of assisting hygroscopically in the dispersal of the spores; along with this we get the provision of mechanisms for the dehiscence of the capsule by means of a lid or of valves, or both, often accompanied by the formation of thickening fibres in the cells of the capsule-wall (already indicated in *Boschia*).

In *Riccia* the developing sporogenous cells readily absorb food

from the thallus tissue which surrounds them and from which they are separated only by the delicate single-layered capsule-wall and double-layered calyptra. In *Tessellina* the capsule-wall is separated by several layers of tissue (the two inner layers belonging to the calyptra) from the chambered assimilating tissue of the involucre, but the food supply for the developing spores comes mainly from below, and with this fact we may correlate the presence of a few sterile cells among the fertile spore-mother-cells. In *Corsinia* the sporogenous tissue is well raised above the thallus level by the differentiation of a foot, which acts as an absorbing organ, and the nutrition of the spore-mother-cells is further secured by the numerous starch-laden sterile cells mingled with the spore-mother-cells and exceeding them in number. The protection of the

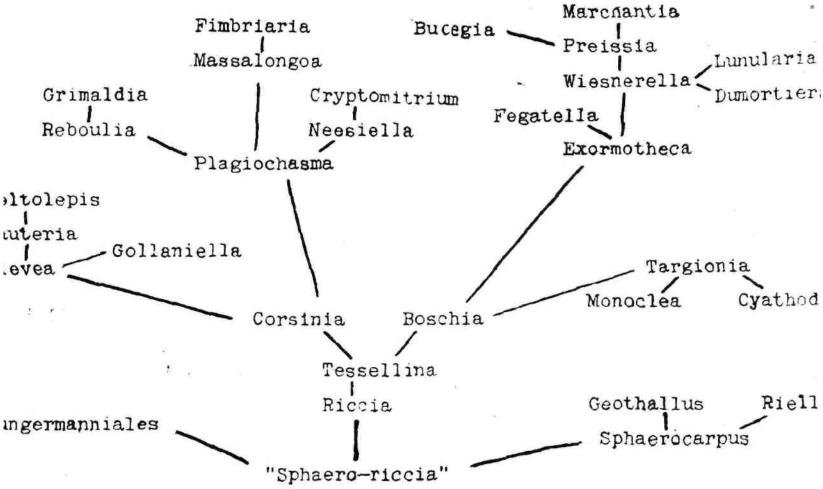

Fig. 29.—Phylogeny of the Marchantiales.

developing sporogonium against desiccation—a function performed in *Riccia* by the surrounding thallus tissue—is in *Tessellina* taken over by the involucre and in *Corsinia* by the massive calyptra. This great development of the calyptra, in which *Corsinia* differs from all other Marchantiales, is evidently a biological adaptation to compensate for the inadequate protection afforded by the incipient carpocephalum; in *Boschia* the calyptra is not nearly so thick as in *Corsinia*, but the hood-like involucre covers the fruit more completely, and persists until dehiscence.

In seeking to trace the phylogeny of the Marchantiales (which, according to the views here advocated, may be roughly represented as in the diagram, Fig. 29), we are confronted by difficulties which involve the phylogeny of the Bryophyta as a whole, and which will

be more appropriately discussed later. The study of the geographical distribution of the existing Hepaticæ leads to the conclusion that the thalloid forms at any rate (the Marchantiales and probably also the lower Jungermanniales) are ancient forms. As Campbell (9) has pointed out, the scarcity of fossil Bryophytes may be partly attributed to the delicate and perishable nature of their tissues. At present no conclusions as to the antiquity of the different groups of Bryophyta can possibly be drawn from the very scanty and doubtful Palæozoic remains that have been referred to provisional genera like *Marchantites* and *Muscites*; see Scott's summary (58). The earliest known undoubted fossil Bryophyte is a *Marchantia*-like form (*Marchantites*) found at least as far back as the Jurassic. Judging from the habitats of the existing forms, the only liverworts that might be expected to occur in the Palæozoic rocks are the shade-loving, hygrophilous, and epiphytic species, belonging chiefly to the leafy Jungermanniales. The existing Marchantiales are much more completely adapted to land life, and to life in open and exposed situations, than are the Jungermanniales. Xerophilous forms occur in all the groups of Hepaticæ, but the proportion of such forms is largest in the Marchantiales.

The habitats of the Marchantiales are also of interest in considering the question whether the existing members of this group really form an ascending series starting with Ricciaceæ, or whether the Ricciaceæ, and perhaps also the Corsiniaceæ, are to be regarded, on the other hand, as reduced forms. The only genus of Marchantiales which clearly shows reduction in both gametophyte and sporophyte is *Cyathodium*, and as Lang (35) has pointed out, this genus "is to be regarded as primarily a form adapted to shade conditions rather than as a hygrophyte." In this respect *Cyathodium* forms a contrast to the markedly hygrophilous genera *Dumortiera* and *Monoclea*, in which there is no evident reduction in the sporophyte though the thallus shows extensive or even complete degeneration of the air-chamber layer. In the Ricciaceæ we have a number of hygrophilous species (*Riccia crystallina* and its allies), and in two cases a terrestrial species has a free-floating aquatic form, either swimming (*R. natans*, the aquatic form of *R. lutescens*) or submerged (*R. fluitans*, the aquatic form of *R. canaliculata*), but the only liverwort which fruits under aquatic conditions is *Riella*, and *Riella* is almost certainly derived from a *Sphærocarpus*-like form by adaptation to submerged aquatic life, and cannot be regarded as a primitively aquatic type.

Whether or not the simple structure of the *Riccia* sporophyte is due to reduction, correlated with the sunken position of the spore-fruit in the thallus tissue, remains an open question. On the whole it seems probable that *Riccia* has been derived from a form not unlike *Sphærocarpus* by elaboration of the thallus as an adaptation to life in more exposed and less hygrophilous surroundings, leading in several species to marked xerophily—shown by the large overlapping purple ventral scales and the formation of perennating tubers. But there is a somewhat wide gulf between *Riccia* and the Sphærocarpales, despite the close agreement in the structure and mode of branching of the apical growing-point, the development of the sexual organs, and the embryogeny; for in *Geothallus* and *Riella*, and even in *Sphærocarpus* itself, we find a marked tendency towards the differentiation of a leafy shoot which is characteristic of the Jungermanniales. Campbell suggested that the three great phyla of Hepaticæ (Marchantiales, Jungermanniales, and Anthocerotales) may be derived from a primitive form (Lotsy's "Sphæroriccia") which combined the simple thallus of *Sphærocarpus* with a *Riccia*-like sporophyte. And, as pointed out by Tansley (63), the Protobryophytes probably arose, by restriction of spore-production to the fertilised egg, from algal ancestors "which possessed archegonia as their female organs, and zoosporangia or aplanosporangia as asexual organs, with no regular alternation of generations, but with the power of bearing sporangia or sexual organs according to temporary conditions, just as is the case in so many green algæ." Assuming that the sporogonium of *Riccia* is primitive, it is of great interest as showing the first step in the progressive sterilisation of a simple spore-fruit formed by segmentation of the fertilised egg.

As already stated, the sporogonium does not reach a very high grade of development in the Marchantiales. This arrest of the sterilisation process is evidently correlated with the fact that in the Marchantiaceæ the stalked carpocephalum carries up the sporogonia into the air and thus renders unnecessary the development of a long sporogonial seta or of more elaborate mechanisms for spore dispersal, such as are found in the Jungermanniales. Only in the peculiar genus *Monoclea* is the capsule elevated on a long seta, as in the Jungermanniales; as already stated, this may be correlated with the extremely hygrophilous mode of life of this genus. In the Corsiniaceæ and Targioniaceæ there is no special means of raising the sporogonium above the general level of the thallus, but these plants do not grow in such moist situations, *Targionia* being in fact

a xerophyte. Besides, there can be little doubt that the spores of many of the Marchantiales are dispersed by water rather than by air-currents. In this connexion, some interesting observations are made in a recent paper by Yeates (70), with reference to the distribution and dispersal of some British representatives of the Marchantiales and thalloid Jungermanniales; though it must be remembered that these groups are very poorly represented in Britain, and hence conclusions drawn from the scanty Hepatic flora of this country can hardly be applied to the liverworts as a whole. Still, Campbell notes the apparently complete absence of Hepaticæ from the new flora of Krakatau, as an indication that the spores of these plants are not generally well adapted for wind dispersal.

In considering the inter-relationships of the Marchantiales, the writer has adopted the view that the group forms an ascending series, starting from *Riccia* and culminating in *Marchantia*, though including some genera which show unmistakeable evidences of reduction in the gametophyte or the sporophyte.

The opposing view, according to which the Marchantiales show wholesale reduction, starting from a type like *Marchantia*, so that the genus *Riccia* represents not a primitive form but the lowest member in a descending series of reduction forms, gains considerable support from Goebel's recent study of the remarkable genus *Monoselenium*.[1] In 1849 there appeared in Griffith's "Posthumous Papers" (*Notulae ad plantas asiaticas*, Part 2) a brief diagnosis of a liverwort which has apparently been lost sight of entirely since that time, or which has been regarded as a *Cyathodium*. Goebel, who has re-discovered and thoroughly investigated the plant, shows that *Monoselenium tenerum* undoubtedly belongs to the Marchantiaceæ. The thallus has no trace whatever of air chambers, but it bears small ventral scales and tuberculate as well as smooth-walled rhizoids. The antheridia and archegonia are borne on receptacles and the plant is monœcious, the male receptacles standing just behind the female receptacles. The latter usually terminate the growth of a thallus-lobe, but are sometimes seated on the dorsal side of the thallus. The male receptacle is at first sessile on the thallus, but is sometimes raised later on a very short stalk, which has, however, no rhizoid-furrow. The receptacles of both kinds are of the "Composite" type. In the male receptacle the antheridia

[1] Goebel, K. Archegoniatenstudien, XIII. *Monoselenium tenerum*, Griffith. Flora, 1910, pp. 43-97.

are developed in centrifugal order on the upper surface; the oldest antheridia occupy the centre of the receptacle, while the marginal tissue remains embryonic and gives rise to new antheridia, though there is apparently no definite arrangement in rows answering to a number of growing-points. The under side of the male receptacle bears scales and rhizoids. Immediately below and in front of the developing receptacle there appears an adventitious branch, which continues the forward growth of the thallus, so that the receptacle (which arises in the first instance as a terminal, *i.e.*, apical, structure) is shifted on to the dorsal side of the thallus. This continuation-branch then proceeds, either at once or after giving rise to a tract of thallus-tissue, to develop a female receptacle. The latter shows from four to ten groups of archegonia, each group being surrounded by an involucre and containing as many as twelve archegonia; the groups are separated by lobes bearing scales and rhizoids, which occur also on the lower part of each involucre. The ripe sporogonium strongly resembles that of the Corsiniaceæ, having a spherical capsule and a short "foot"; the capsule-wall consists of a single layer of unthickened cells—except at the apex where there is a cap composed of several layers, some of which have rudimentary thickening-fibres; the sterile cells mixed with the spores are short and retain their chlorophyll, and are either unthickened or show rudimentary annular or spiral fibres; the spores remain united in tetrads when ripe; the seta remains undeveloped, the capsule is not exserted from the involucre, and the spores escape merely by the irregular breaking-up of the capsule-wall.

We may regard *Monoselenium* as a reduced form, the reduction extending to all the organs but being exhibited by the different organs in varying degrees. The thallus resembles that of *Monoclea* in having no trace of an air-chamber zone, but the ventral scales, instead of being reduced to unicellular or filamentous gum-papillæ, resemble rather those of *Dumortiera* or *Cyathodium*—which, as we have seen, are certainly reduced forms. In the structure of the sporogonium, *Monoselenium* forms a perfect connecting-link between the genera *Corsinia* and *Boschia*; sterile cells resembling those of *Corsinia*, *Sphærocarpus*, and *Riella*, occur in the same capsule with rudimentary elaters like those of *Boschia*. But the most remarkable feature of *Monoselenium* is Goebel's discovery that sexual receptacles of the "Composite" type may become shifted on to the dorsal side of the thallus, so as to occupy the same position as the archegoniophores of *Clevea* and *Plagiochasma*. The writer has already

suggested that "the carpocephala of all the Marchantiaceæ, except *Clevea* and *Plagiochasma*, represent branch-systems." This suggestion was based on the fact that several archegonia were found to be produced from each growing-point in the receptacles of various genera (*Sauteria*, *Peltolepis*, *Grimaldia*, *Neesiella*, *Reboulia*, *Fimbriaria*) in which the archegonia were formerly regarded as occurring singly in each involucre. Goebel's observations on *Monoselenium* not only support this suggestion, but show that there is no need to exclude *Clevea* and *Plagiochasma* from the general interpretation of the archegoniophore as representing invariably a branch-system. It is clear that a "Composite" receptacle, in which the sexual organs are developed in centrifugal order from several growing-points and which is therefore a branch-system, need not necessarily terminate the growth of the thallus, but may come to occupy the sameposition as the "dorsal outgrowth" type of receptacle which Leitgeb regarded as contrasting strongly with the "branch-system" type.

Goebel proceeds to elaborate the view that those members of the Marchantiales in which the sexual organs are borne in receptacles seated on the upper side of the thallus, or in which these organs are borne dorsally but not grouped into receptacles at all, are reduced and not primitive forms. He also suggests that the *Riccia* sporogonium, in which sterilisation is limited to a single peripheral layer of cells is not a primitive type of sporophyte, but is the lowest term in a descending series of forms in which the elaters become reduced to short sterile cells and finally are not developed at all. But further discussion of the wider questions raised by the study of the Marchantiales may be deferred until a later stage. As regards the systematic position of *Monoselenium*, it is by no means easy to determine the affinities of this aberrant and greatly reduced genus; Goebel shows that its archegoniophore differs in several apparently essential respects from that of *Dumortiera*, while the far-reaching reduction of the sporogonium sets it apart from every other known Marchantiaceous genus.

It is interesting to note that androgynous receptacles, in which antheridia and archegonia may even occur intermingled, as well as occupying different portions of the same receptacle, occur in *Monoselenium*. In this peculiarity the genus resembles *Dumortiera*, though androgynous receptacles occur also in *Preissia* and have recently been described by Cutting[1] in a species of *Marchantia*.

[1] Cutting, E. M. "On Androgynous Receptacles in *Marchantia*." Annals of Botany, vol. 24, 1910, pp. 349-357.

The occurrence of these "abnormal" receptacles is of interest from various points of view; for one thing, they demonstrate the homology which exists between the male and female receptacles throughout the Marchantiaceæ, and which could otherwise be inferred only from the facts of comparative morphology.

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III. ANACROGYNOUS JUNGERMANNIALES.

The Jungermanniales were divided by Leitgeb (40, 41) into a lower series (Anacrogynæ) and a higher series (Acrogynæ), for which Underwood (70) proposed the terms Metzgeriaceæ and Jungermanniaceæ respectively. The Acrogynæ owe their name to the fact that the apical cell of the main axis or of a branch eventually becomes an archegonium, so that apical growth is arrested by the production of a group of archegonia. It is also characteristic of the Acrogynæ that at least the sexual branches, and in the vast majority of cases the entire plant-bodies, are differentiated into stems and leaves, and that the young leaf divides primarily by a radial wall into two cells which in many cases grow out independently for a longer or shorter time and frequently give rise to two deeply separated lobes. Many of the Anacrogynæ also show differentiation into stem and leaves, but the leaf-primordium never shows the initial division into two lobes; and in all the forms placed here, excepting the Calobryaceæ, the archegonia are borne on the upper side of the thallus or of the stem, the apical growth of which is therefore not necessarily arrested by the development of these organs.

This two-fold division of the Jungermanniales is largely an artificial one, and as a matter of fact we find among the Anacrogynæ a series of types in which the development of the archegonia becomes, as it were, shifted nearer and nearer to the apex, while we have also a series of striking parallel developments, along independent lines, leading to the differentiation of a leafy shoot from a simple thalloid plant-body. The Jungermanniales form a single phylum, the boundaries between the systematic families are in most cases badly defined, and probably in no other group of plants do we find such striking and abundant examples of parallelism or homoplasy.

The general characters of the Jungermanniales, as contrasted with the Marchantiales, have already been enumerated, and we have seen that the two phyla are connected by the synthetic group of the Sphærocarpales, which combine several of the distinctive characters of the Jungermanniales and Marchantiales, though on the whole probably standing nearer to the latter, and at the same time presenting peculiar features of their own.

The Anacrogynæ may be divided into four families, whose inter-relationships will be discussed later. This division differs somewhat from that adopted by Schiffner (54); the genus *Monoclea* has, in this series of articles, been transferred to the Marchantiales, while two genera discovered recently (*Makinoa* and *Cavicularia*) are here dealt with, and some minor changes in classification are suggested, such as the splitting up of *Pallavicinia* into two genera (*Blyttia* and *Mörckia*) and the restoration of the old division of *Hymenophytum* into two genera (*Podomitrium* and *Umbraculum*).

ANEURACEÆ.

This family (Schiffner's Metzgerioideæ) contains four genera—*Aneura* with over 150 species, *Metzgeria* with about 70, *Podomitrium* and *Umbraculum* (united by many writers into a single genus, *Hymenophyton*) with 2 species each. One of the most characteristic features common to these four genera is the restriction of the antheridia and archegonia to short special branches, which arise from the margin of the thallus in *Aneura*, but are ventral in origin in the other genera.

The genus *Aneura* received its name from the fact that in the European species the thallus differs from that of *Metzgeria* in not being sharply differentiated into a cylindrical mid-rib and a thin single-layered wing on either side of it, but in reality more than half the species of *Aneura* now known do show this differentiation, which is present in all the species of the other three genera. In several of these winged and often epiphytic species of *Aneura* there is considerable differentiation of the thallus branches.[1] In *A. bogotensis* the branches arising on one side of the creeping axis remain short and cylindrical and become attached to the substratum, while those on the other side of the axis branch repeatedly and give rise to broad flattened assimilating organs. In *A. eriocaula* and *A. fucoides* the lower branches serve as organs of attachment and, like the main axis itself, remain cylindrical, while the upper branches are erect, spreading, flattened and differentiated into mid-rib and wings. In other species there are various adaptations for the retention of water by capillarity. In *A. hymenophylloides* the branches have strongly incurved margins, forming water-sacs. In *A. fuegiensis* the same purpose is served by longitudinal lamellæ which project from the lower surface of the thallus. The genus is of great interest as showing the possibilities of the simple thallus,

[1] Several of these species are figured by Goebel (17).

with its forking or (more frequently) monopodial and pinnate branching, in the way of that differentiation into axis and leaves which has arisen repeatedly along independent lines among the lower Jungermanniales.

Many of the species of *Metzgeria* are epiphytes, and among

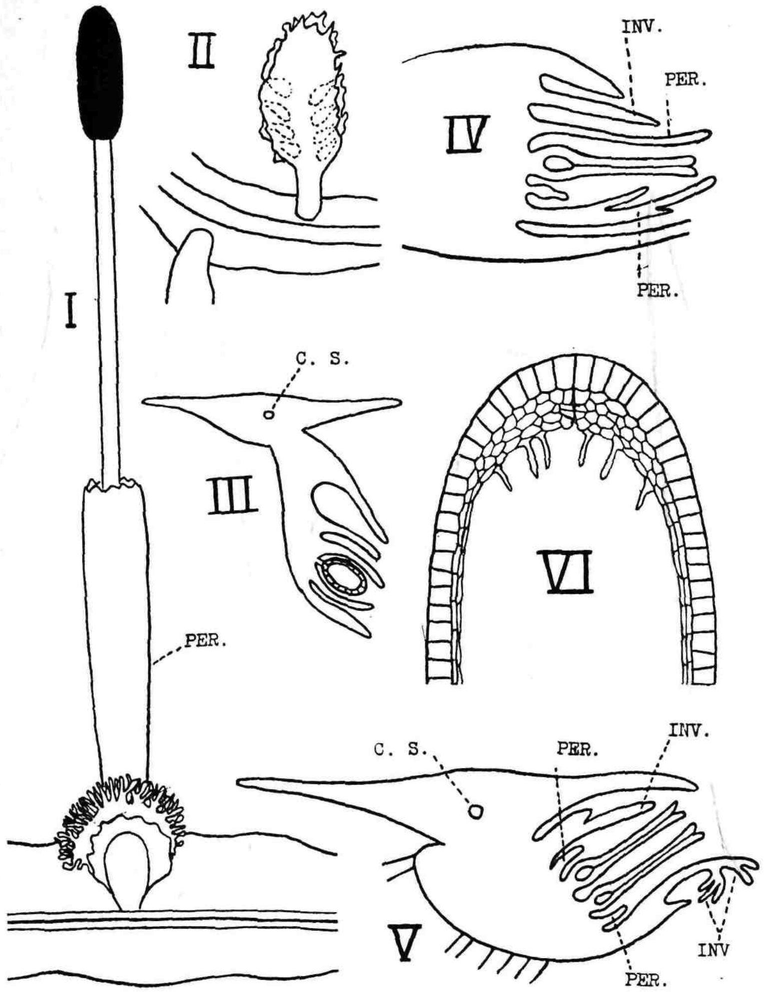


Fig. 30. *Podomitrium (Hymenophytum) phyllanthus.*—I, Part of a female plant from below, showing a female branch with ripe sporogonium; II, Part of a male plant, from below, showing two antheridial branches; III, Transverse section of a male plant traversing an antheridial branch; IV, Longitudinal section of an archegonial branch, after fertilisation, showing the developing perianth within the involucre; V, Similar section showing the appearance of the perianth before fertilisation; VI, Upper part of a longitudinal section through a ripe capsule, showing the apical thickening of the capsule-wall. *c.s.*, conducting strand; *inv.*, involucre; *per.* perianth.

these there is an interesting form, *M. saccata*, which bears curious water-sacs. Each sac is formed by the margin of the wing becoming in certain places rolled over towards the underside and then by active superficial growth converted into an ovoid structure with its opening directed towards the lower side of the mid-rib; from the convex outer surface of the sac rhizoids frequently grow out.

A third line of differentiation of the thallus is seen in *Umbraculum*. In the allied genus *Podomitrium*, e.g. *P.* (*Hymenophytum*) *phyllanthus* (Fig. 30), ordinary apical branching occurs, but numerous branches arise from the mid-rib on the underside of the thallus. The basal portion of each branch is nearly cylindrical, but the distal portion develops on either side a broad wing, which frequently narrows again and becomes obsolete at the end of the branch; the rhizoids spring chiefly from the stalk-like basal portion. In *Umbraculum*, e.g., *U.* (*Hymenophytum*) *flabellatum*, however, the creeping, wingless rhizome-like basal portion, to which the rhizoids are confined, gives off erect branches which are at first cylindrical, but towards the top become winged and then undergo repeated dichotomy to form a fan-like assimilating branch-system (Fig. 31). Goebel (26) has shown that when this highly differentiated plant is grown in moist air and feeble light the fan-like shoots may produce rhizoids and their growing-points may grow out to form wingless runners or rhizomes. The axis or mid-rib in *Podomitrium* and *Umbraculum* is traversed by a strand of narrow elongated cells with thick walls which bear slit-like pits. The axial bundle of a ventral branch is not continuous with that of the parent-axis, but is separated from it by a zone of thin-walled cells, hence these ventral branches readily become detached.

In all three genera the sexual organs are borne on special short branches. In *Aneura* these arise from the margin of the thallus and are merely lateral branches whose growth in length is arrested by the formation of the antheridia or archegonia, but in the other genera these organs are confined to short ventral branches arising from the sides of the mid-rib. The antheridia are either sunk in cavities in the tissue of the male branch, or are covered by the inrolled margins of the branch, or protected in both these ways. In *Podomitrium*, the male branch has a cylindrical stalk and an expanded distal antheridium-bearing portion (Fig. 30, II.); in *Metzgeria*, its margins are rolled up so as to form a sac; in *Umbraculum*, the male branch is reduced to a sessile cushion-like outgrowth of the mid-rib (Fig. 31). There is thus a gradual reduction in the

structure of the male branch in the four genera, reaching its limits in *Umbraculum.*

In *Aneura* and *Metzgeria* the female branches are very much

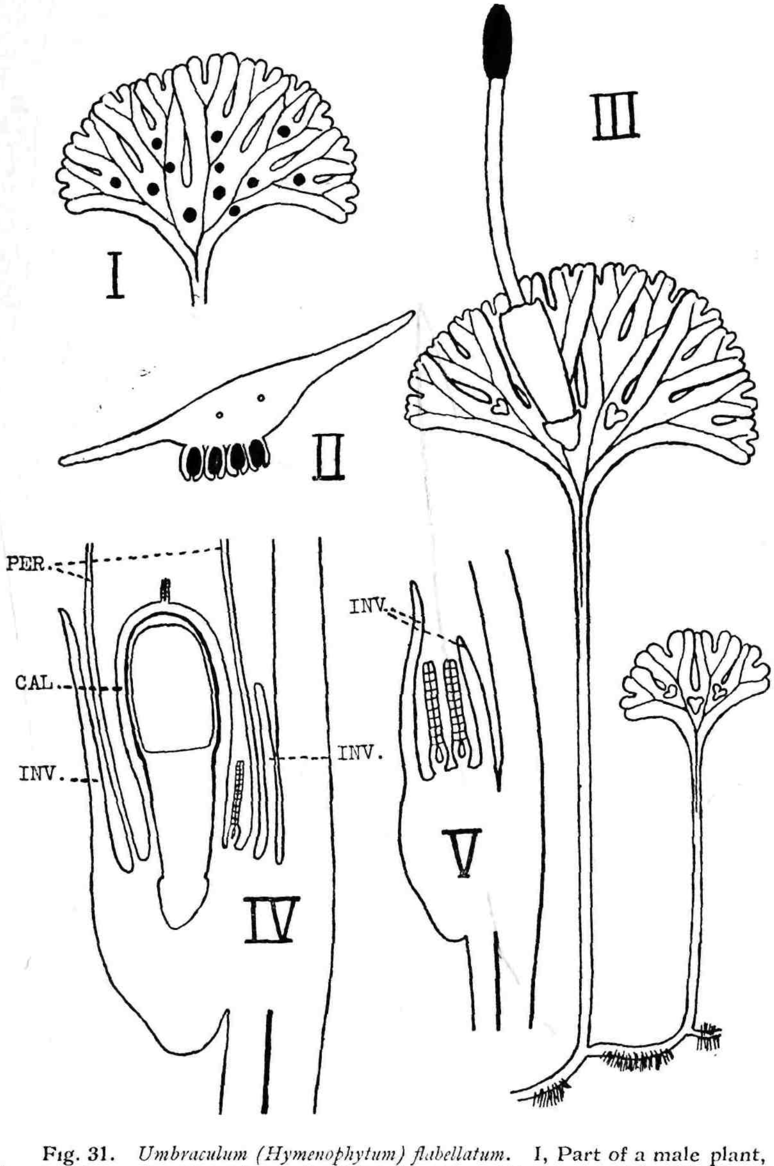


Fig. 31. *Umbraculum (Hymenophytum) flabellatum.* I, Part of a male plant, from below, showing the antheridial branches (diagrammatic); II, Cross section of a male plant, showing the antheridia; III, Part of a female plant, with archegonial branches and a sporogonium; IV, Longitudinal section of an archegonial branch with a nearly ripe sporogonium; V, Similar section of a branch with unfertilised archegonia. *cal.*, calyptra; *inv.*, involucre *per.*, perianth.

like the male branches. In *Podomitrium* the female branch is short but differentiated into a cylindrical portion which bears a narrow wing; on the expanded end of the branch are developed the archegonia, surrounded by a collar-like envelope (involucre) with fringed margins (Fig. 30, I.) In *Umbraculum* the wing of the female branch is more fully developed, and the involucre is reduced to a scale instead of forming a bell-like sheath (Fig. 31, III.) In *Aneura* and *Metzgeria*, the sporogonium is protected until ripe by the calyptra, which is a thick fleshy structure, often bearing on its surface the unfertilised archegonia. In *Podomitrium* and *Umbraculum* there arises within the involucre a second sheath (perianth) surrounding the archegonia; in the former genus the perianth is laid down before fertilisation occurs, in the form of a few scales arranged in a ring, the scales being later carried up by active growth of the tissue at their base (Fig. 30, IV., V.), but in *Umbraculum* the perianth arises after fertilisation in the form of a ring-like outgrowth of the tissue surrounding the archegonia (Fig. 31, IV.)

In all four genera, the sporogonium has a well-developed seta which rapidly elongates when the capsule is mature and thrusts the latter through the calyptra, the capsule then opening, typically, by four valves extending from apex to base. The early stages in the embryogeny have only been studied in *Aneura*, and the following account is based upon the writer's examination of the sporogonia of *A. pinguis* and *A. latifrons*. The lower (hypobasal) cell formed by the first transverse division of the oospore either undergoes no further development or divides by a few walls, chiefly transverse, to form a short appendage; hence practically the whole sporogonium (capsule, seta, foot) is formed from the upper (epibasal) half of the segmented oospore, the foot arising as a club-like swelling of the lower end of the seta. The epibasal cell first divides, as a rule, by a transverse wall, which separates the capsule from the seta. Then intersecting vertical divisions set in, together with further transverse divisions in both the upper and lower epibasal cells, so that there are now several superposed tiers consisting each of four cells. Up to this point, *Aneura* follows what is probably, with slight differences in detail, the development characteristic of all the Jungermanniales. In *Aneura*, as in other Anacrogynæ which have been investigated, the capsule is derived from the uppermost tier of four cells, but in many Acrogynæ one or more of the tiers formed in the lower epibasal series may contribute to the formation of the capsule besides forming the seta. In both the capsule- and the seta-forming tiers,

divisions next occur which cut off four axial rows of cells (the endothecium) from a layer of outer cells (the amphithecium). The further development of the *Aneura* capsule, from this stage onwards, has been well described by Goebel (23) and by Bower (4). The amphithecium gives rise to the capsule-wall, which at a very early stage becomes two-layered and remains so throughout its development; the whole of the rest of the capsule is derived from the four primary endothecial cells. The tissue formed by the early divisions of the endothecium is uniform, but this tissue soon becomes differentiated into two portions, which Goebel characterises as "independent meristems." The peripheral cells, forming a U-shaped layer or band in a longitudinal section of the capsule, divide rapidly and contain dense protoplasm, with chloroplasts but no starch; the central cells, continuous above with the apical portion of the capsule-wall, undergo relatively few divisions, are more transparent and contain starch, but no chlorophyll. As Bower has clearly shown, the cells produced by the inner portion of the peripheral band, as development proceeds, assume the characters of the central cell-group, so that the latter becomes more extensive, and the densely-staining peripheral region becomes reduced to a thin peripheral fringe around the sides and base of the large central tissue. The peripheral fringe, which produces the spores and free elaters and to which the term archesporium might therefore be restricted, now begins to grow actively and becomes more sharply marked off from the sterile columella, which hangs downwards into the cavity of the capsule. As the development of the capsule proceeds, the size of the sterile columella, as compared with the capsule as a whole, diminishes, so that in a ripe capsule of *A. pinguis* the columella extends only about one-third the distance from apex to base of the capsule. The columella probably serves to nourish the fertile tissue during the early development of the capsule, since its cells contain starch, but as the capsule ripens the starch disappears from this sterile tissue and the cells become elongated and acquire ring-like fibrous thickenings. Ordinary free elaters, pointed at each end, are developed amongst the spores, but from the surface of the columella (which is also termed the "elaterophore") there grow out elater-like cells ("fixed elaters") which project into the mass of spores and free elaters.

When the capsule is pushed up through the calyptra by the elongation of the seta, the capsule-wall and also the columella or "elaterophore" split into four parts, along lines of thin-walled cells

which are recognisable (both in the capsule-wall and the columella) before the capsule is ripe. Thus each of the four valves of the capsule-wall has attached to its tip a quarter of the columella, with its tuft of fixed elaters, and as the four valves bend outwards each of the four masses of spores and elaters moves into a vertical position on the valve, and the spores, together with the loose or free elaters, are actively flicked outwards. Hence the columella, after splitting into quarters, brings about the active dispersal of the spores.

Metzgeria differs from the other three genera in having spherical instead of ovoid or cylindrical capsules, but the structure is very much the same as in *Aneura* ; the elaterophore is not quite so well developed, and its cells have only here and there irregular thickenings on their walls, instead of the well developed half-rings found in the larger elaterophore of *Aneura*.

In *Podomitrium* and *Umbraculum* the capsule-wall consists of an outer layer of large nearly cubical cells, and one or two inner layers of elongated and flattened cells. According to Andreas (1), these inner cells are continuous with the apical pad or cap, lying below the layer of large outer cells, at the top of the capsule, and Goebel (26) therefore distinguishes this cap from the columella of *Aneura* and *Metzgeria* as being of different origin, comparing it to the apical thickening of the capsule-wall found in various Marchantiales. In the latter group, however, the apical cap cannot always be interpreted as arising by periclinal division of the otherwise single-layered capsule-wall, and it is not easy to determine the exact origin of the cap. In *Fegatella* and *Reboulia*, according to the writer's investigation of these genera (10, 11), this cap is derived from the archesporium, the apical portion of which exhibits sterilisation comparable to that seen in *Aneura*. In any case, however, the capsule-wall in Marchantiales is not differentiated until a relatively late stage ; that is, the separation of the archesporium is not determined by the first periclinal divisions in the young capsule. In *Umbraculum* (*Hymenophytum*) *flabellatum* the cap, or elaterophore, splits into four portions, as in *Aneura* and *Metzgeria*, one remaining attached to the tip of each valve of the dehisced capsule and bearing a number of fixed elaters. In *Podomitrium* (*Hymenophytum*) *phyllanthus*, however, the capsule dehisces by from two to four slits, but these do not extend to the apex, where the valves are coherent. In *Umbraculum* the large outer cells of the capsule-wall have localised but indefinite band-like thickenings on the radial cell

walls, but in *Podomitrium* these cells are uniformly thickened and bear no definite fibres; in both genera there arise from the bottom of the capsule cavity isolated fixed elaters of varying form, some being short and without fibrous thickenings, others long and elater-like.

In *Aneura* the developing sporogonium is protected by a massive and fleshy calyptra formed by vigorous growth of the tissue of the female branch; this active growth extends to the tissue underlying the fertilised egg, where a projecting bulbous mass is formed, bearing rhizoids. The calyptra carries up the scales which grow out around or among the archegonia, and usually also the unfertilised archegonia themselves. In *Metzgeria* the calyptra is not so massive, and is formed chiefly from the venter of the fertilised archegonium.

In the Aneuraceæ, asexual reproduction is effected in various ways. The simplest is the separation of ordinary branches by the dying away of the old portions of the thallus; in *Podomitrium* and *Umbraculum* the severance of the branches from the parent axis is facilitated by the fact that the strand of thick-walled cells in the ventral branch is not continuous with that in the parent stem.

The asexual reproduction of *Metzgeria* by means of gemmæ has recently been investigated by Evans (15), who has shown that each of these bodies (consisting usually of a single layer of cells) arises from a single cell of the parent thallus, either from a cell of the wing or from one of the cortical cells of the mid-rib. The superficial cell about to produce a gemma projects beyond its neighbours; the outer wall of the cell is ruptured, but the protruding protoplast becomes covered by a layer of gelatinous material which probably represents a modification of the inner part of the original outer wall and which is deposited prior to the rupture of the wall. The projecting cell thus formed, either with or without a preliminary division into a lower cell which does not enter into the formation of the actual gemma, usually undergoes at once divisions which cut out a two-sided apical cell; in some cases the gemma has two growing-points from the earliest stages of its development. The details vary greatly in different species, as shown by Evans.

In several species of *Aneura*, gemmæ are formed in a somewhat different manner. The contents of a superficial cell of the thallus separate from the wall, and the rounded-off protoplast acquires a cell-wall and divides into two cells. The two-celled gemma escapes by rupture of the free outer wall of the mother-cell. As compared with *Metzgeria*, the further development of the gemma in *Aneura* is deferred until after the gemma is set free.

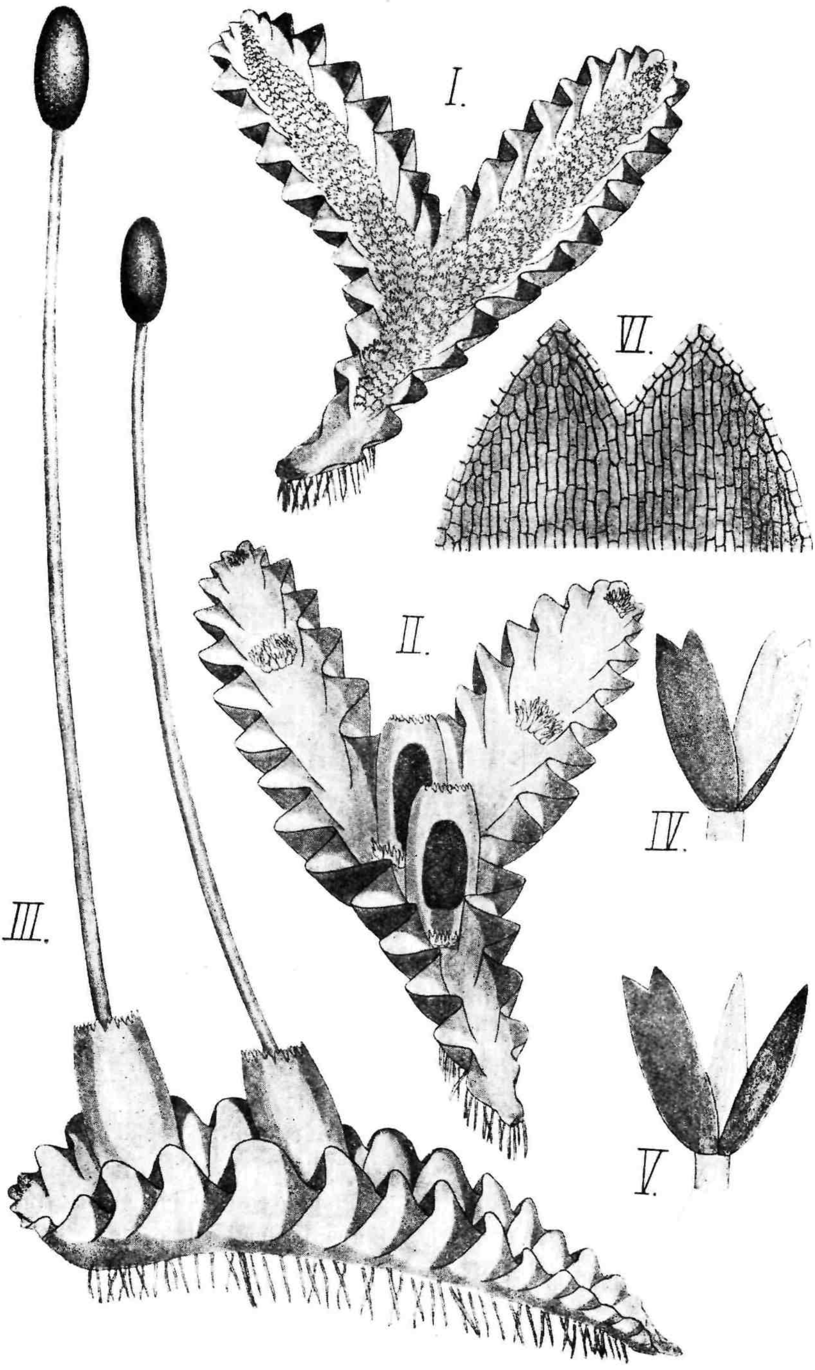


Fig. 32. *(For description see next page).*

Fig. 32. *Mörckia flotowiana.* I, Male plant, from above, showing the broad midrib covered by toothed scales (male bracts), each of which forms a hood over an antheridium, ×5. II, Female plant, from above. Six archegonial groups are seen. In the four younger groups the archegonia are surrounded by the involucral leaves (female bracts), the perianth not yet being developed; in the two older groups the perianth is represented as being transparent, to show the half-ripe sporogonium within it, ×5. III, Female plant, bearing two ripe sporogonia; in each case the seta has become elongated, carrying up the capsule, which has not yet dehisced, ×5. IV and V, Ripe capsules, showing different modes of dehiscence, ×8. VI, Upper portion of one of the valves of a capsule, ×40.

BLYTTIACEÆ.

Under this name it is proposed here to designate a family, agreeing in part with Spruce's family "Leptotheceæ," in which Schiffner includes three genera—*Pallavicinia*, *Symphyogyna*, and *Monoclea*. The first-named genus should, however, be split into the two genera *Blyttia* and *Mörckia*; while *Monoclea* has been removed to the Marchantiales. The recently discovered genus *Makinoa* is probably best placed here, so that our family Blyttiaceæ includes the four genera *Blyttia*, *Mörckia*, *Symphyogyna*, and *Makinoa*. The name Leptotheceæ was suggested originally by Spruce (60) to include the three genera placed in it by Schiffner and also the genus *Calobryum*, on account of the absence of ring-fibres from the cells of the capsule-wall and the incomplete separation of the capsule-valves at dehiscence.

The Blyttiaceæ are distinguished from the Aneuraceæ chiefly by the fact that the sexual organs are born on the upper side of the ordinary thallus and not on special short branches. The four genera of Blyttiaceæ differ in so many respects that it will be convenient to describe them separately.

In *Blyttia*, the thallus is differentiated into a cylindrical midrib and a single-layered wing on either side. In twenty of the thirty known species, the whole thallus is attached to the substratum. In some cases, e.g., *B. Lyellii*, the margin of the wing is entire, but in several species belonging to this "Repentes" section of the genus, e.g., *B. longispina*, *B. xiphioides*, the margin bears regular appendages which, as shown by Goebel (22, 24), may be regarded as representing leaves, since they are formed with great regularity at the growing-point, which it is their primary function to protect. In the remaining species, forming the section "Erectæ" or "Dendroides," *e.g.*, in *B. decipiens* which was fully investigated by Farmer (16), the thallus consists of a creeping cylindrical basal portion, consisting of the midrib alone, and an erect distal winged portion which undergoes repeated dichotomy, the branches spreading out like a fan—exactly as

in *Umbraculum*. The midrib is traversed by an axial strand of pitted cells, and Tansley (68) showed that in *B. Lyellii* eosin solution passes along this strand more rapidly than through the surrounding tissue

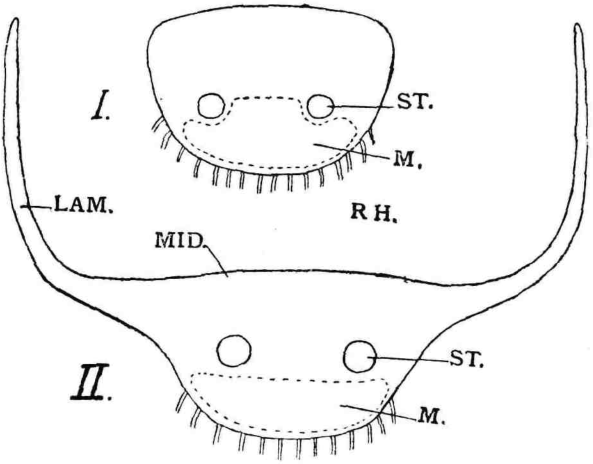


Fig. 33. *Mörckia flotowiana.* I, Transverse section through base of plant. II, Similar section taken further forwards. *st.*, conducting strands of midrib; *m.*, mycorhizal zone; *rh.*, rhizoids; *lam.*, lamina or wing of thallus; *mid.*, midrib. ×25.

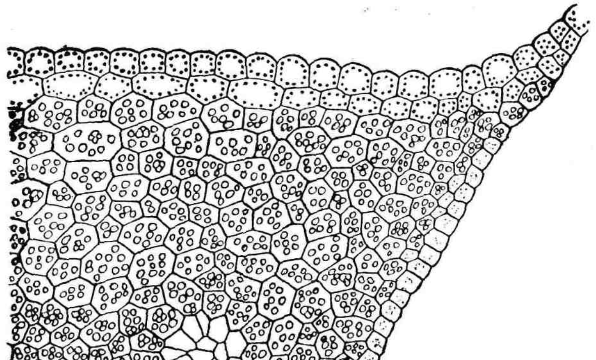


Fig. 34. *Mörckia flotowiana.* Part of Fig. 33, II, ×70.

of the midrib, so that we have here a rudimentary conducting strand. The antheridia are borne in two rows along the midrib on the upper side of the thallus, each antheridium being spherical, shortly-stalked,

and covered from behind by a hood-like scale. The archegonial groups, also borne dorsally, are each surrounded by a short cupule-like involucre formed from a series of toothed scales and by a much longer perianth which is laid down before fertilisation occurs, exactly as in *Podomitrium*; within the perianth is the calyptra, which is about the same length or a little longer and which usually bears near the top the unfertilised archegonia. The capsule has much the same structure as in *Podomitrium*, and it usually opens by two to four slits, the valves generally remaining attached at the top, where there is a cap-like mass of tissue.

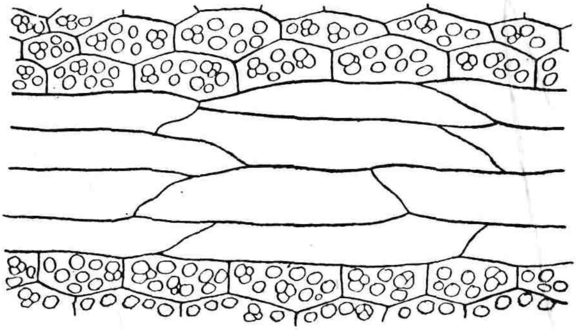


Fig. 35. *Mörckia flotowiana.* Part of a longitudinal section of the midrib, traversing one of the conducting strands. On either side of the elongated hyaline strand-cells are the cortical cells, packed with starch grains. ×180.

In *Mörckia*, the thallus is always creeping, as in the "Repentes" section of *Blyttia*, with a broader midrib and less sharply defined wings, the latter being frequently wavy, (Fig. 32) but never showing incipient differentiation of leaves. In *M. Flotowiana* the midrib contains two strands of elongated cells (Figs. 33-35), but these are of much simpler structure than the strands of *Blyttia*, *Symphyogyna*, *Podomitrium*, and *Umbraculum*. There are small filamentous appendages on the lower side of the thallus, especially at the growing point (Fig. 36), and in *M. Blyttii* numerous small leaf-like appendages are borne on the *upper* surface along the midrib. These appendages are similar to the scales which in all species of *Blyttia* and *Mörckia* cover the antheridia. In *Mörckia* the antheridia are sometimes developed in more than two rows, and the scales covering them are more or less fused together, so that the antheridia appear to be sunk in chambers (Fig. 36) in the upper tissue of the thallus. The involucre and perianth in *Mörckia* resemble the corresponding structures in *Blyttia*, but the capsule-wall has from three to five layers of small cells within the outer layer of large cells (Fig. 37).

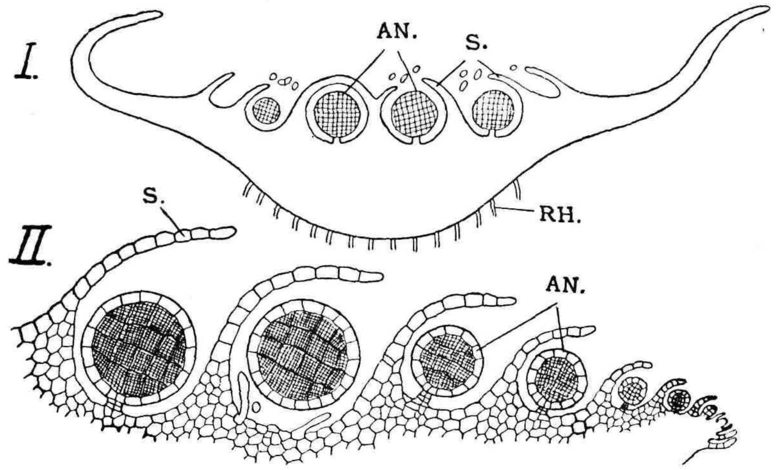


Fig. 36. *Mörckia flotowiana.* Transverse (I) and longitudinal (II) sections of a male plant showing the antheridia (*an.*) and the scales (*s.*) covering them; *rh.*, rhizoids. I ×25, II ×70.

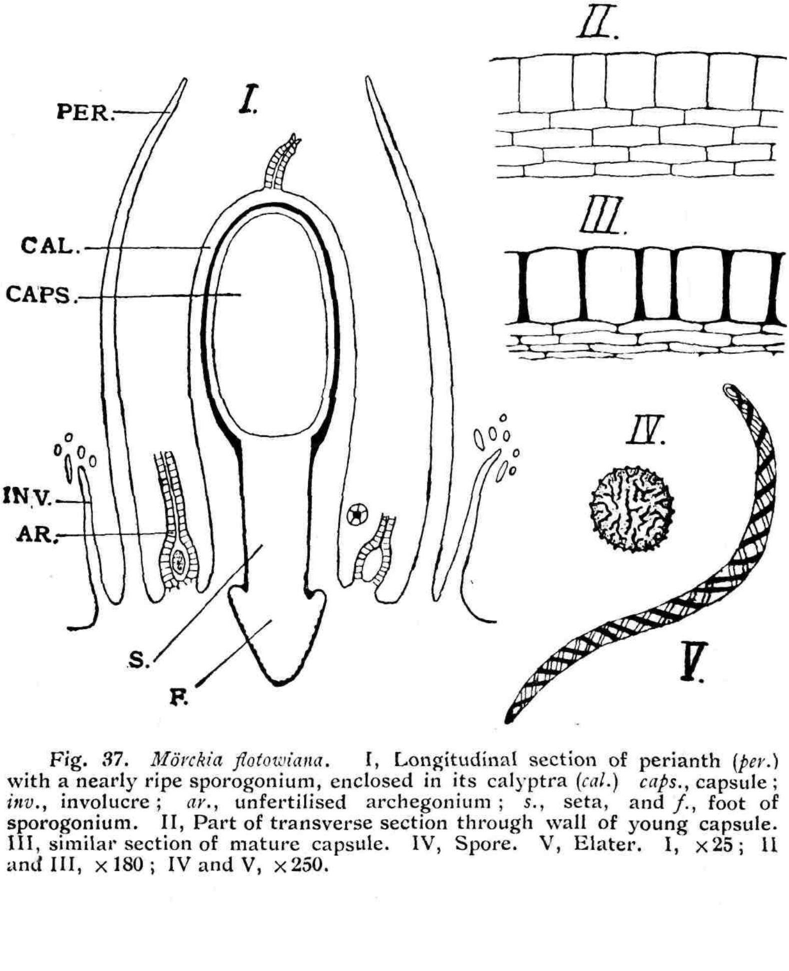


Fig. 37. *Mörckia flotowiana.* I, Longitudinal section of perianth (*per.*) with a nearly ripe sporogonium, enclosed in its calyptra (*cal.*) *caps.*, capsule; *inv.*, involucre; *ar.*, unfertilised archegonium; *s.*, seta, and *f.*, foot of sporogonium. II, Part of transverse section through wall of young capsule. III, similar section of mature capsule. IV, Spore. V, Elater. I, ×25; II and III, ×180; IV and V, ×250.

The capsule-wall splits along more or fewer of the four dehiscence lines laid down previously, hence the number of valves varies from two to four; the valves do not cohere at the top, as a rule.

Symphyogyna (Fig. 38) differs from *Blyttia* and *Mörckia* in having no perianth; the calyptra, instead of being thin as in these

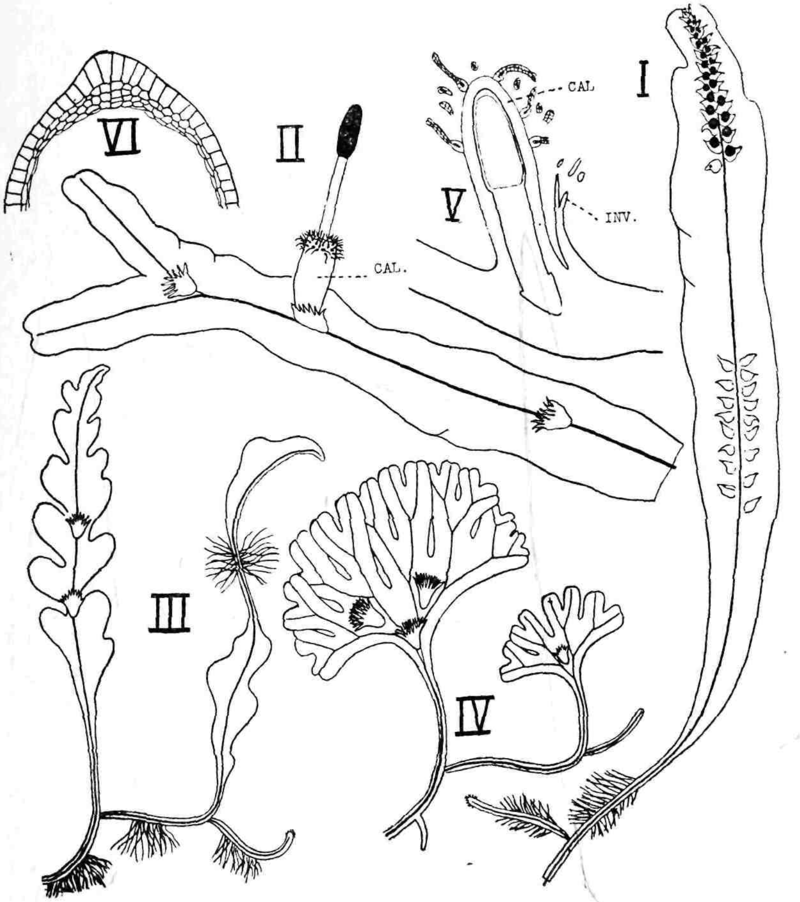


Fig. 38. *Symphyogyna.* I, A male plant of *S. brasiliensis.* II, a fruiting female plant of the same species. III, A female plant of *S. Brongniartii.* IV, A female plant of *S. hymenophyllum.* V, Longitudinal section of female branch of *S. brasiliensis*, showing a developing sporogonium. VI, Longitudinal section of upper part of capsule of *S. brasiliensis*. *cal.*, calyptra; *inv.*, involucre.

genera, is massive and bears on its upper portion the unfertilised archegonia; the involucre consists of a single scale. In practically every other respect, however, *Symphyogyna* shows an extraordinarily close resemblance to *Blyttia*, and it is very difficult to distinguish between sterile plants of the two genera. Moreover, the species of

Symphyogyna fall into two sections, corresponding exactly to the "Repentes" and "Dendroideæ" sections of *Blyttia.* Among the creeping species, some have the margin of the wing entire; in others there are marginal teeth; in others again, the wing is sinuately lobed; and in some species the wing may be absent from one side of the midrib, though present on the other side. The "Dendroid" species have a basal creeping portion and an erect portion consisting of fan-like dichotomising branches, like the corresponding species of *Blyttia.* If we regard *Podomitrium* and *Umbraculum* as forming sections or sub-genera of the genus *Hymenophytum*, we have a striking parallelism between the three genera, each having flat creeping species and erect dendroid species. This parallelism was pointed out by Farmer in his memoir on *Pallavicinia (Blyttia) decipiens* (16). In *Symphyogyna*, as in *Blyttia*, the midrib is traversed by an axial strand of lignified and pitted cells; in some species there are two or even three of these strands (29). The capsule has the same structure as in *Blyttia*; after being thrust through the thick calyptra which envelops it, the capsule opens by valves which remain coherent at the top.

In the Japanese genus *Makinoa*, which was originally described by Stephani (65) as a *Pellia* but later recognised as an independent genus, and described by Miyake (51) and by Schiffner (59), the thallus is very similar to that of *Mörckia*, having a wavy margin and filamentous ventral scales. The antheridia are collected into a definite receptacle, occupying a depression on the upper side of the thallus, and each antheridium is sunk in a chamber which is open above and is separated from the neighbouring chambers by a partition two cells thick. The archegonial group is covered by a lobed hood-like scale, as in *Symphyogyna*, and the young sporogonium is protected by a massive calyptra formed by outgrowth of the thallus tissue and bearing on its surface the unfertilised archegonia, as in *Symphyogyna* and *Aneura.* The ellipsoid capsule opens, as a rule, by two valves which may remain coherent at the top. The capsule-wall is two-layered, the outer cells being large and having thickening bands on the radial cell-walls, while the inner cells are narrow and thin-walled; at the apex of the capsule there is a cap consisting of three or four layers of cubical cells, and to this cap are attached long elater-like filaments, differing from the ordinary free elaters in having no fibrous thickenings.

CODONIACEÆ.

This family is distinguished from the Blyttiaceæ chiefly by the

characters of the capsule, which is spherical (ovoid in *Blasia*) and when ripe, dehisces by four valves extending from apex to base (except *Fossombronia* and *Petalophyllum*, where the wall breaks up into irregular plates). The capsule-wall consists typically of two layers of cells (four in *Blasia* and *Treubia*), well-developed fibrous thickenings being usually present in either the outer or the inner cells, or in both. There is usually a basal columella or elaterophore but sometimes this is represented only by a few elongated elater-like cells at the base of the capsule-cavity. In addition to the calyptra, there is usually a tubular envelope around the sporogonium, in addition to the calyptra, but only in *Calycularia* is there an involucre in addition to a perianth. Except in *Pellia* and *Calycularia,* there is a definite differentiation of the plant-body into stem and leaves.

The simplest type of vegetative structure is found in *Pellia*, in which the thick median portion of the thallus passes rather gradually into the thinner lateral wings. In *P. epiphylla* many of the cells have broad ribbon-like thickenings on the walls; usually each cell has only a single band, and in a longitudinal section of the

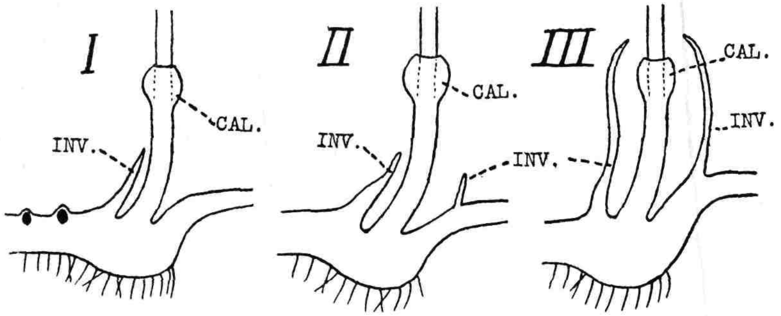


Fig. 39. Diagrammatic longitudinal sections through the calyptra and involucre of (I) *Pellia epiphylla*, (II) *P. Neesiana*, (III) *P. calycina*.

thallus the bands are seen to be arranged in lines running from the upper to the lower side. These bands are also found in the thallus of *P. Neesiana*, but are absent from *P. calycina* ; both these species differ from *P. epiphylla* in being diœcious. Though *Pellia* is so largely studied as a type in elementary teaching, the descriptions given in text-books are mostly very inaccurate in various points; this is partly due to the fact that the three species just mentioned—the only species of the genus, and all occurring in Britain—are frequently confused w th each other. The antheridia are sunk separately in cavities, scattered over the upper side of the thick median region of thallus. The archegonia are developed in groups,

each group becoming sunk in a pocket-like cavity which opens in front, the archegonia being directed horizontally and accompanied by short mucilage-hairs. The margin of this pocket shows differences characteristic of the three species. In *P. epiphylla* and *P. Neesiana* it forms a short involucre beyond which the calyptra of the ripe sporogonium extends for some distance, whilst in *P. calycina* it forms a long bell-like envelope enclosing the calyptra. In *P. epiphylla* the involucre or pocket-margin grows out only on the posterior side, forming a hood-like scale, but in *P. Neesiana* it grows out all round as a short collar-like sheath (Fig. 39).

In the young capsules of *Pellia*, after the capsule-wall has become differentiated as an outer layer of large cells and (usually) two inner layers of small cells, but before one can distinguish between the spore-mother-cell and those which will later form the free elaters mingled with the spores, the inner tissue (endothecium) shows a fairly sharp separation into two portions—a sterile basal portion extending from the bottom of the capsule and spreading out fanwise as seen in longitudinal section, and a fertile portion which extends over the top of the columella-like basal tissue. The columella, or elaterophore, consists of elongated cells, forming a bundle of fixed elaters. In *P. calycina* (23, 36) the fixed elaters of this bundle (about a hundred in number) are much longer than the free elaters and often reach more than half-way up the capsule; like the free elaters which are mingled with the spores, they usually have a double spiral band. In *P. epiphylla* the fixed elaters are fewer in number (thirty to fifty), shorter, thicker, and furnished with from one to four spiral bands. *P. Neesiana* resembles *P. epiphylla* in the structure of the capsule; in these two species the inner layers of the capsule wall bear ring-like fibres, which are lacking in *P. calycina*. When the capsule opens the four valves move outwards and downwards, exposing the mass of spores and loose elaters, which are held together for a time by the tuft of fixed elaters, the mass then becoming loosened by the hygroscopic movements of the elaters and gradually shaken out.

The basal tuft of fixed elaters in the capsule of *Pellia* arises in the same way as the apical sterile tissue forming the elaterophore of *Aneura* and *Metzgeria*. The differences in the mature structure of the columella and in its behaviour when the capsule dehisces, are clearly connected with the difference in position. In *Aneura* the apical columella remains coherent until the capsule dehisces, when it splits into four portions, one of which remains attached to

the tip of one of the valves of the capsule-wall; whilst the basal columella of *Pellia* splits up into long elater-like cells and forms a mop-like tuft which holds the spores and free elaters loosely together, and assists in their general dispersal.

In *Calycularia*—a genus which, as Schiffner has pointed out, (57, 58), has generally been confused with *Mörckia*—the thallus resembles that of *Pellia* in form, but there is a sharper distinction between midrib and wings, and on the lower side of the midrib there are developed, chiefly at the growing point, small leaves comparable with the ventral scales of the Marchantiales or the amphigastria of the Acrogynæ. The archegonial group is protected by a series of scales, and, after fertilisation, there arises within these a bell-like perianth, as in *Mörckia*. The capsule, however, strongly resembles that of *Pellia* in structure; the wall consists of two layers of cells bearing fibrous thickenings, and at the base of the cavity there is a tuft of fixed elaters, exactly as in *Pellia*; the ripe capsule opens by a varying number of valves.

Noteroclada (*Androcryphia*)[1] is also closely allied to *Pellia*, but here the plant-body is differentiated into stem and leaves, the latter being nearly semi-circular and inserted by a broad base on the cylindrical stem. The growing-point has a three-sided apical cell; each lateral segment gives rise to a leaf, whose insertion is at first transverse to the long axis of the stem, but later becomes shifted so as to be horizontal, and eventually the anterior edge of the leaf lies below the posterior edge of the leaf in front (succubous leaf-arrangement); from each ventral segment there grow out four mucilage-hairs, representing a ventral scale or amphigastrium. The leaves are one cell thick, except at the base, where there are several layers of cells. Apart from the different form of the apical cell and the different organisation of the vegetative organs, *Noteroclada* is clearly related to *Pellia*; each antheridium is sunk in a cavity of its own, and the capsule agrees very closely with that of *Pellia*—there is a basal tuft-like elaterophore, and the spores begin to germinate and become multicellular before the dehiscence of the capsule, which takes place by four valves. This premature germination of the spores, however, occurs in several unrelated Hepatics, e.g. *Fegatella* and *Dendroceros*. In *Noteroclada* the archegonia are not sunk in a cavity, as in *Pellia*, but arise from the

[1] Professor Goebel, in a recent letter to the writer, announces that he has been fortunate enough to obtain living material of this interesting and rare type, and that its structure and development are under investigation at Munich.

upper surface of the stem and are protected by the young leaves at the stem-apex; but this difference is clearly correlated with the fact that *Pellia* is thalloid while *Noteroclada* is foliose. Stephani (66) says that *Noteroclada* is so near *Pellia* that it should perhaps be included in that genus, and that it is practically a *Pellia calycina* with stem and leaves instead of simple thalloid plant-body.

In *Blasia* there is a broad stem bearing on either side a row of large leaves lying in the same plane as the broad midrib or stem, and not so sharply separated from it as in *Noteroclada*. In addition to the leaves, *Blasia* developes an extraordinary diversity of appendages—*Nostoc*-auricles and amphigastria on the lower surface, curious flask-like gemma-receptacles and star-like gemmæ on the upper surface. The amphigastria on the lower side and the star-like gemmæ (5) on the upper are alike in structure, being cell-plates attached by a short stalk at the centre; the former stand singly at the junction of leaf and stem, the latter are scattered over the upper side of the thallus and on being detached give rise to new plants. The long-necked gemma-flasks have been described and figured already in this journal (7). The *Nostoc*-appendages (17, 41, 53, 70), of which there are usually two to each leaf, when ready for infection by *Nostoc*, are rounded pockets, each formed from a cell which projects from the thallus and divides transversely, cutting off a terminal club-shaped slime-secreting cell, around which the auricle grows like a hood by division of the underlying cell. After the entrance of the *Nostoc*, the opening closes up and the whole auricle increases in size; as the *Nostoc* chains grow, the slime-secreting cell projects into the cavity and branches to form a tree-like structure, the ramifications of which doubtless absorb nourishment from the algal cells. The flask-like gemma-receptacles are probably modified archegonial receptacles, since archegonia are sometimes found in these flasks. The antheridia and archegonia have the same arrangement and structure as in *Pellia*, but the capsule (1, 52) differs considerably from that of *Pellia*, being elongated and having its basal portion produced downwards as a collar around the top of the seta. There are no ring-like fibres in the capsule wall, which consists of an outer layer of large cells with rodlike thickenings on the radial walls, and two or three inner layers of flattened and thin-walled cells; at the base of the capsule there are a few fixed elaters, representing a rudimentary elaterophore.

The Japanese genus *Cavicularia* closely resembles *Blasia* in

vegetative structure, having similar leaves, *Nostoc*-appendages, amphigastria, and antheridia, but its sporogonia have not been discovered. Two kinds of gemmæ are produced, according to Schiffner (56); some are lens-shaped, others spherical, and both kinds are produced in crescent-like receptacles resembling those of *Lunularia*. The archegonia are developed in receptacles exactly like those containing the gemmæ, the latter being produced on the sterile female plants; sometimes, in fact, the archegonia occur in groups in the gemma-receptacles themselves. It seems probable that in both *Blasia* and *Cavicularia* we have an example of thc replacement of spore-production by asexual propagation; *Blasia* is more often found with gemma flasks than with fruits, and apparently in *Cavicularia* fruits are very rarely formed and have not yet been discovered.

In *Fossombronia*, which is the largest genus of Codoniaceæ, having nearly fifty species, the plant has the same general habit as that of *Noteroclada*, but the stem is broader, and sometimes the leaves are no more sharply marked off from it than in the case of *Blasia*. There are small ventral scales near the growing point (33), serving for the protection of the latter and soon perishing; the underside of the stem bears numerous rhizoids, which usually have a characteristic deep reddish-violet colour. In some species, e.g., *F. longiseta*—recently described in detail by Humphrey (35)—the stem is thickened to form a tuber in which food is stored; while in *F. tuberifera*—discovered by Goebel (17)—the plant periodically grows down into the soil, the leaves becoming greatly reduced in size and the end of the stem swelling to form a tuber which passes through a resting stage and afterwards resuming growth to form an ordinary leafy shoot. The antheridia are scattered singly over the stem, close to the leaf-bases, and are sometimes protected by a scale growing from the stem tissue immediately behind the antheridium. The archegonia are developed in small groups, on the middle or sides of the stem; after fertilisation an envelope (perianth) arises, as in *Noteroclada*, as a ring-like outgrowth from the stem tissue surrounding the group. The capsule-wall has an outer layer of unthickened cells and an inner layer of cells bearing thick half-ring fibres, often very irregularly arranged. The elaters are short and there are usually no fixed elaters, or very few, at the base of the capsule. Sometimes the ripe capsule dehisces by four valves, but more often the upper portion of the wall breaks up into irregular plates which are thrown off, leaving the mass of spores and elaters held in the saucer-like lower portion of the wall.

The curious genus *Petalophyllum* (8, 48, 69) is closely allied to *Fossombronia*, but in vegetative structure it strongly resembles *Geothallus*. The plant is fan-shaped, expanding from a narrow cylindrical basal portion. On either side of the stem there is a

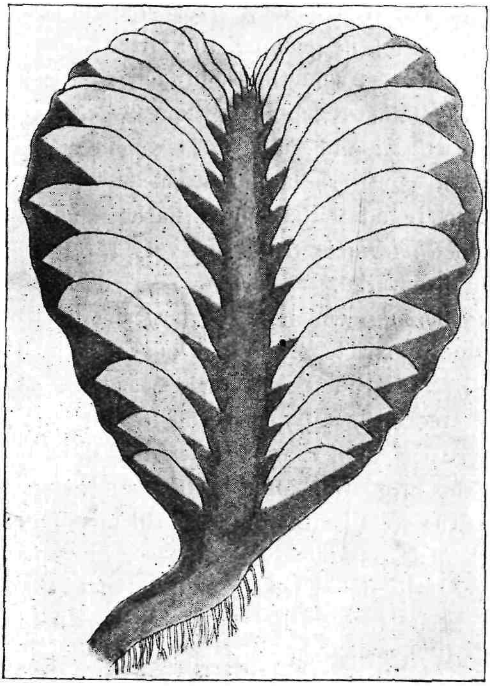


Fig. 40. *Petalophyllum ralfsii*. Plant as seen from above. ×8.

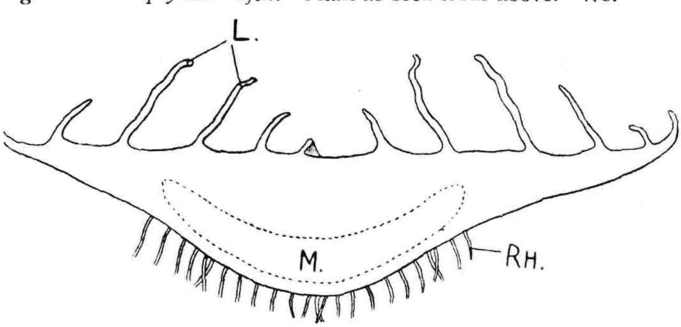


Fig. 41. *Petalophyllum ralfsii*. Transverse section through the middle of the leaf-bearing region of the plant. *L.*, leaves; *M.*, mycorhiza; *Rh.*, rhizoids, ×20.

horizontal wing bearing vertical laminæ, which run forwards and outwards (Figs. 40, 41). The lamellæ are one cell thick and are often arranged with great regularity in two series, one on either

side of the middle line. The plant grows near the sea, and periodically becomes buried in the sand, forming a tuber in which food is stored (Fig. 43). The leafy portion of the plant dies down,

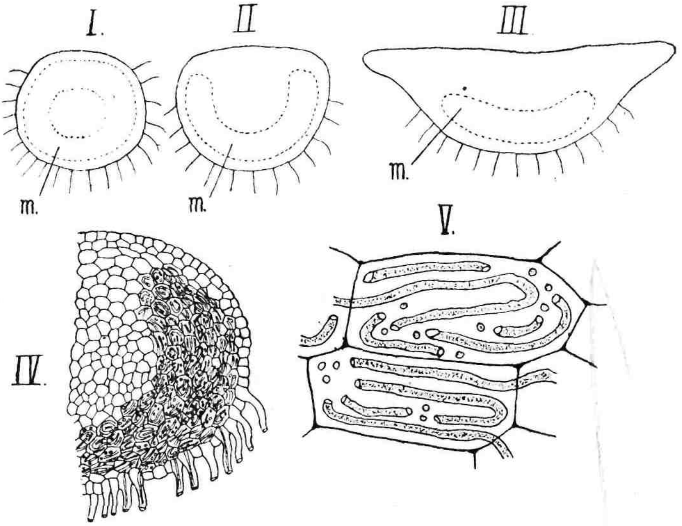


Fig. 42. *Petalophyllum ralfsii.* I-III, Successive transverse sections of the stem, ×20; *m*, mycorhizal zone. IV, Part of I, ×50, showing fungal hyphæ traversing the rhizoids and ramifying in cells of mycorhizal zone. V, Two cells containing hyphæ, ×350.

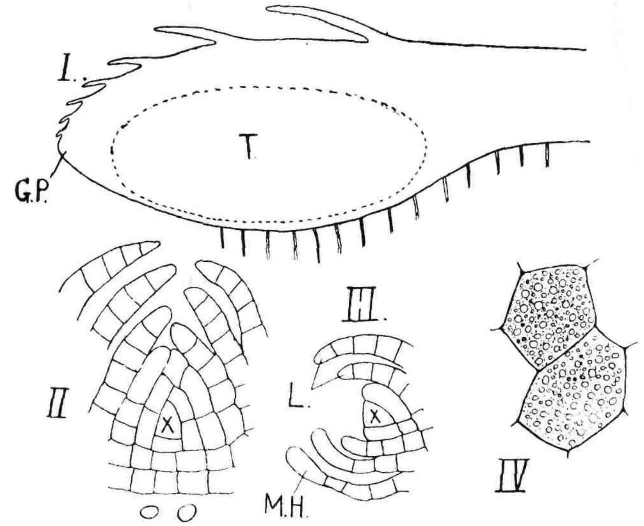


Fig. 43. *Petalophyllum ralfsii.* I Longitudinal section through apex of of stem, showing the tuberous swelling (T) behind and below the growing-point (G.P.). II, Transverse section of growing-point, showing the apical cell (X). On either side are the young leaves (L.); below are two mucilage-hairs in cross-section. *III*, Part of a longitudinal section through the growing-point. *L.*, leaves; *M.H.*, mucilage-hairs. IV, Two cells in the tuber, showing densely granular contents. I, ×20; II, III, ×150; IV, ×350.

and when growth is resumed the first-formed portion of the new shoot consists of stem only, but later the leaves appear and the stem expands laterally to form the broad wing which carries the leaves (laminæ) on its upper side. The antheridia are developed in a group behind the apex and are protected by small scales. The archegonial group becomes surrounded by an envelope formed in the same way as in *Fossombronia*, and in the structure and dehiscence of the capsule *Petalophyllum* closely resembles that genus.

Treubia insignis, a very beautiful plant discovered by Goebel in Java (20) and later in New Zealand (26), is the largest of the dorsiventral leafy Anacrogynæ, and shows the mostly highly diffentiated leaves. The apical cell is three-sided, as in *Noteroclada* and *Petalophyllum*, and the leaves, at first inserted transversely on the stem, eventually become oblique, the insertion of each leaf sloping downwards and forwards (succubous). At the front of each leaf, on its upper side, there is a small lobe or scale which projects inwards over the upper surface of the stem and forwards beyond the insertion of the leaf (Goebel's "Organography," Figs. 165 and 166). The antheridia and archegonia are developed on the sides of the stem and are protected by the scales of the leaves. There is no perianth, but the developing sporogonium is protected by a thick calyptra, which, as in *Aneura*, is formed from the stem tissue around the archegonial group. The spherical capsule dehisces by four valves; the wall consists of three or four layers of cells, the outer cells being large and flattened and devoid of thickenings, while those of the inner layers have numerous half-ring fibres, or, in some cases, a spiral fibre; at the base of the capsule there are a few fixed elater-like elongated cells, representing a rudimentary elaterophore.

CALOBRYACEÆ.

This family, consisting of the two genera *Haplomitrium* and *Calobryum* is one of the most remarkable and interesting among the Bryophyta. The former genus has a single species (*H. Hookeri*) apparently confined to Europe (27, 34, 46, 52); *Calobryum* has three species, found in Java and New Guinea, in Japan, and in South America respectively (17, 21, 54, 66).

The Calobryaceæ differ considerably in vegetative structure from all other Hepaticæ. The plant consists of a branching underground rhizome-like portion, without rhizoids; from this leafless rhizome there spring erect leafy shoots, each growing by a three-

sided apical cell and consisting of a cylindrical stem and spirally arranged leaves. Müller (52) in his description of *Haplomitrium*, states that the leaves are irregularly disposed on the stem, but Stephani (66) states that in both genera there is a distinction between two rows of obliquely inserted leaves, and a third row of transversely inserted leaves, the latter corresponding to the ventral leaves or amphigastria of the Acrogynæ. Goebel (21) describes the same arrangement in *Calobryum Blumei*, where the transversely inserted row, consists of leaves only half as large as those in the other two rows.

In *Haplomitrium* the shortly-stalked ovoid antheridia are borne, usually in groups of two or three, in the axils of the upper leaves of the male plant; according to Stephani they are never found in the axils of the transversely inserted leaves (amphigastria), but Müller (52) says that they are arranged all round the stem and may also occur on the stem surface without any relation to the leaves. Gottsche in his classical memoir (27) gives the same account as Müller. The archegonia are also developed in the axils of the uppermost leaves of the female plant, these leaves being usually larger than the others; there is no involucre or perianth, but the sporogonium is protected by a large cylindrical calyptra. The development of archegonia does not arrest the apical growth of the shoot; the apical cell is not used up in the formation of an archegonium, and sometimes the apical growth of the shoot is resumed after the formation of a sporogonium. The oblong capsule usually opens by two or three valves; the wall consists of a single layer of cubical cells, each having a single thickened ring-like band extending over the horizontal and tangential walls of the cell, instead of being set transversely to the long axis of the capsule as are the ring fibres in the capsule-wall of other Hepaticæ.

In *Calobryum*, which has the same general habit as *Haplomitrium*, the leaves are apparently arranged more definitely in three rows, and both the antheridia and the archegonia are developed in groups on the flattened and broadened apex of the stem. In both cases the group of sexual organs is surrounded by three large spreading leaves, so that the plant has a close superficial resemblance to the male "flower" of *Funaria* or *Mnium*. In the development of the archegonia, the apical growth of the plant is arrested, hence *Calobryum* is definitely acrogynous. The sexual organs, calyptra, and sporogonium have the same structure as in *Haplomitrium*.

Phylogeny of the Anacrogynæ.

With the exception of the Calobryaceæ, the four families into which we have here divided the Anacrogynæ are somewhat artificial. The classification and phylogeny of the Anacrogynæ present great difficulties. It might be expected that the great diversity in both gametophyte and sporophyte shown by the genera of Anacrogynæ would make it comparatively easy to arrange them in a natural classification, but it is just this diversity, together with the frequent occurrence of parallel developments in different lines, that baffles our attempts to frame a satisfactory arrangement. For instance, the genera *Aneura* and *Pellia* present the simplest type of gametophyte along with the most advanced type of sporogonium, if one may assume that the undifferentiated thallus is really the primitive type of plant-body and that the sporogonium which shows the earliest and most extensive sterilisation of "potentially sporogenous tissue" is the highest type of sporophyte. Both of these assumptions have been challenged, the former by Wettstein and the latter by Goebel and others, but the questions raised will be considered later when discussing the general phylogeny of the Bryophyta.

Various writers have attempted to draw sharp distinctions between "thallus-lobes" and "true leaves" in the Anacrogynæ, but these supposed distinctions are based upon somewhat narrow morphological ideas derived from the study of the Acrogynæ. For instance, Stephani (66) describes *Blasia*, and even *Treubia* (62) as having a "lobed thallus," though he applies the term "leaves" to the appendages of the axis in *Fossombronia* and *Noteroclada*. Yet in all four genera the appendages arise in essentially the same way at the growing-point, an appendage being formed from each lateral segment cut from the apical cell and having therefore a definite position with reference to the axis.

In the Anacrogynæ the growth of the plant-body is always referable to a single apical cell, the form and mode of segmentation of which show great diversity in the various genera and even differ in different species of the same genus. Still, the mode of apical growth is of interest and even of value, in helping us to understand the morphology of the plant-body, with special reference to the

origin of the differentiation into stem and leaves of the presumably primitive thallus—a differentiation which has clearly arisen in several distinct lines and by several distinct methods.

The simplest type is, apparently, the "two-sided" apical cell, that is, a cell from which two sets of lateral segments are cut off, alternately right and left. An apical cell of this kind occurs in *Aneura*, *Metzgeria*, *Podomitrium*, *Umbraculum*, *Symphyogyna*, and *Fossombronia*. In each case the apical cell is triangular as seen in a surface view of the growing-point (or a horizontal section through it) and only two sets of segments are cut from it, but there are differences in detail as regards the relation of the apical cell to the tissue formed by the further divisions of the segments. In *Metzgeria*, for instance, the apical cell is nearly square as seen from the front, and nearly hemispherical as seen in a vertical longitudinal section through the growing-point. In the other genera, however, a smaller portion of the apical cell is exposed on the upper and lower sides, the dorsal and ventral tissue covering it to a varying extent. This is due to the more active growth of the upper and lower portions of each lateral segment, the midrib in these genera being more massive than in *Metzgeria*. In *Fossombronia*, this rapid growth of the segments is especially marked, and the apical cell has the form of a spindle, elongated vertically, when seen from the front. In *Metzgeria*, *Podomitrium*, *Umbraculum*, and *Symphyogyna*, each segment divides first by a vertical wall into an inner (adaxial) and an outer (abaxial) cell; the latter divides only by walls vertical to the plane of the thallus and forms the single-layered wing, while the former divides also by walls parallel with the surface of the thallus and contributes to the formation of the midrib. In the wingless species of *Aneura*, all the cells formed from the segments divide by both horizontal and vertical walls, so that the thallus is several layers in thickness. In *Fossombronia*, each lateral segment divides first by two superposed horizontal walls; the upper and lower cells contribute to the formation of the stem, while the middle cell grows out to form a leaf.

In *Blyttia*, *Mörckia*, *Blasia*, and *Pellia calycina*, the apical cell is wedge-shaped, four sets of segments being cut from it—dorsal and ventral segments as well as right and left lateral segments. In a vertical longitudinal section through the growing-point, the apical cell is triangular, while in surface view or horizontal section it is usually four-sided. The dorsal and ventral segments contribute to the thick axial portion of the plant-body. In *Blyttia* the lateral

segments divide in much the same way as in *Metzgeria*; in *Pellia calycina* their division resembles what is seen in the wingless species of *Aneura*; and in *Mörckia* we have a transition between the two types, the thick median portion of the thallus usually thinning out into the wing on either side more abruptly than in *Pellia calycina*. In *Blasia*, the lateral segments divide in practically the same way as in *Fossombronia*, horizontal divisions giving three superposed cells of which the dorsal and ventral add to the stem tissue while the middle cell forms a leaf.

In *Pellia epiphylla* the apical cell is semi-circular in a vertical longitudinal section through the growing-point, and there are cut from it three sets of segments, two lateral and one posterior, the latter extending the whole depth of the thallus and only later dividing into dorsal and ventral cells. As Campbell (6) has pointed out, this type has probably been derived from the wedge-shaped type (with four sets of segments) "by a gradual increase in the angle formed by the dorsal and ventral walls of the apical cell, which finally became so great as to form practically one plane." The midrib is usually decidedly thicker, vertically, in *Pellia calycina* than in *P. epiphylla*, and the differences in the form of the apical cell and its mode of segmentation may perhaps be connected with this difference in the depth of the midrib in the two species.

Finally, in *Noteroclada*, *Petalophyllum*, *Treubia*, and the Calobryaceæ, we have a tetrahedral cell, similar to that found in most of the Acrogynæ and Mosses, from which three sets of segments are cut off in spiral succession. In the Calobryaceæ, which grow erect and are more or less distinctly radial in symmetry, each segment produces a leaf, but the leaves of one row are frequently, if not always, either larger or smaller than those of the other two rows and further differ from them in being inserted transversely instead of obliquely on the stem, so that even in this group we get the bilateral symmetry and anisophylly which are so characteristic of the Acrogynæ. In the other three genera of Anacrogynæ with a tetrahedral apical cell, the plant grows horizontally and is bilaterally symmetrical, and leaves are only formed from the lateral (strictly, dorso-lateral) segments, though in *Noteroclada* and *Petalophyllum* each ventral segment produces hairs which represent the ventral leaves or "amphigastria" of the typical Acrogynæ. In *Noteroclada*, the upper portion of each dorso-lateral segment contributes to the formation of the stem, while the lower portion grows out to form a leaf; in *Petalophyllum*, each dorso-lateral

segment divides, like the lateral segments in *Fossombronia*, into three superposed cells, of which the dorsal contributes to the midrib and the ventral to the wing on either side of the midrib, while the middle cell forms one of the lamellæ on the upper surface of the wing.

The differentiation of the plant-body into stem and leaves is associated with all the three chief types of apical cell found in the group—the "two-sided" *Metzgeria* type, the "four-sided" or wedge-shaped type, and the tetrahedral type. This fact strengthens the evidence, drawn from other considerations, that leaves have evolved independently in several distinct lines of relationship among the Anacrogynæ. Whatever the form of the apical cell, each lateral segment divides at an early stage into a portion which contributes to the thicker axial region of the plant-body and a portion which grows out and gives rise either to a continuous wing or to a leaf. Absolutely no morphological distinction can be drawn between a plant-body with a midrib and lobed wings, as seen in species of *Symphyogyna*, and one with distinct stem and leaves. We find in the Anacrogynæ every stage in the transition from a thallus with a continuous entire wing to a sharply differentiated leafy shoot, and the differences which are seen in the mature plant-body are differences of degree only. For instance, in *Blasia* the inner or axis-forming portion of each lateral segment grows more actively than is the case in *Fossombronia*, hence in the former genus the stem is broader and the leaves less sharply marked off from it than in the latter. The same explanation may be applied to those species of *Blyttia* and *Symphyogyna* in which the wing is either regularly and deeply lobed or bears regularly arranged filamentous marginal appendages. If the outer portions of the lateral segments grow uniformly, those of successive segments remaining coherent, we get a thallus with or without sharp distinction into midrib and wings; if the outer portion of each segment grows out independently, we get a leafy stem; and between the two extremes we get all stages of transition.

The only Anacrogynæ in which the plant-body is purely thalloid and shows no signs of differentiation into stem and leaf are *Pellia*, *Calycularia*, *Makinoa*, *Mörckia*, and the four genera we have classed under Aneuraceæ. In all these genera there is a more or less marked midrib with a thin wing on either side, though in some species of *Aneura* this differentiation is not shown.

In *Umbraculum* and the "Dendroid" species of *Blyttia* and

Symphyogyna, however, the plant-body is differentiated into a creeping wingless sympodial rhizome and an erect fan-like assimilating portion formed by repeated "dichotomy" of a winged axis. In these three genera, as well as in *Podomitrium*, the axis is traversed by a strand of pitted cells; in *Podomitrium* and in the creeping species of *Blyttia* and *Symphyogyna*, the strand is less strongly developed than in *Umbraculum* and the "Dendroid" species of *Blyttia* and *Symphyogyna*; in the "Dendroid" forms, again, the strand is more bulky in the erect than in the creeping portion of the plant. The observations of Tansley and Chick on *Mörckia hibernica* and *M. Flotowiana* (syn. *M. hibernica*, var. *Wilsoniana*) have already been referred to. In the latter species the writer found (9) that in the new branches produced by plants cultivated in glass-covered dishes in moist conditions (the plants came from sandy flats on the Yorkshire coast), the midrib showed no trace whatever of the two conducting strands which are normally present. It may be noted that several species of *Aneura* show a close approach to the "Dendroid" habit found in the genera *Blyttia*, *Symphyogyna*, and *Umbraculum*, though in *Aneura* the assimilating portion shows pinnate instead of fan-like "dichotomous" branching.

It is clear that both the "Dendroid" habit and the conducting strands have arisen independently in the different genera in which these developments occur. The most striking form of parallelism met with in the Anacrogynæ, however, is that which has led to the differentiation of the plant-body into stem and leaf. This is seen in its simplest form in those species of *Blyttia* and *Symphyogyna* in which the wing of the creeping thallus bears on its margin regularly arranged filamentous outgrowths or teeth, one such outgrowth being formed from each lateral segment of the apical cell. As Goebel (24, 26) has suggested, the primary function of these outgrowths is the protection of the growing-point, and it would seem reasonable to extend this view to account for the evolution of leaves in general. Where no leaf-like outgrowths arise from the lateral segments of the apical cell, the growing-point is provided with gum-secreting papillæ which arise from the cells above or below the apical cell, or from the segments at either side of it, or in all these positions. In many cases, the leaves arise in exactly the same way, the young leaf forming at first a unicellular club-shaped gum-papilla, which by active growth and divisions in the cell that bears it, becomes terminal on a cell-row or a cell-plate. Apart from *Blyttia* and *Symphyogyna*, in which the evolution of leaves only occurs in certain species, and

the leaves themselves are in these species inconspicuous (except at the growing-point) owing to their early loss of individuality, of the eighteen Anacrogynous genera here dealt with, no less than eight are distinctly foliose. The vegetative organisation of these genera (*Noteroclada*, *Blasia*, *Cavicularia*, *Fossombronia*, *Petalophyllum*, *Treubia*, *Haplomitrium*, and *Calobryum*) has already been described in some detail.

The Calobryaceæ stand well apart from the other Anacrogynæ, but the three remaining families are connected by cross-affinities, besides showing parallel developments in the position, investment, and structure of the sexual organs and sporogonia, as well as in the vegetative organs. The Aneuraceæ and Blyttiaceæ have elongated capsules (except *Metzgeria*), with a more or less highly developed apical elaterophore. Only in *Aneura* and *Metzgeria* is this structure an efficient mechanism for active spore-dispersal, for in these genera alone does the capsule-wall regularly split into four valves, each bearing at its tip a quarter of the split-up elaterophore; in the other genera the capsule dehisces by a varying number of valves which usually remain coherent at the tip. In all the genera placed in these two orders, with the exception of *Aneura* and *Metzgeria*, the fibrous thickenings in the capsule-wall are either absent or feebly developed, while the elaterophore is represented by a flattened cap of cells with some elater-like outgrowths hanging down into the cavity of the capsule. Apart from the restriction of the sexual organs to special short branches (lateral in *Aneura*, ventral in the other three genera) there is no constant character separating the Aneuraceæ from the Blyttiaceæ. As regards the investment of the sporogonium, two genera in each family have no well-developed envelopes outside the calyptra, which is massive and fleshy (*Aneura*, *Metzgeria*, *Symphyogyna*, *Makinoa*). A tubular envelope ("perianth") is present in *Podomitrium*. *Umbraculum*, *Blyttia*, and *Mörckia*, surrounding the archegonial group and arising either before or after fertilisation of one of the archegonia; in these four genera there is an additional investment ("involucre") outside the perianth, consisting of a single scale (*Umbraculum*) or of a cupule-like circle of scales. In *Symphyogyna* and *Makinoa*, there is also a single involucral scale, as in *Umbraculum*; in *Aneura* and *Metzgeria*, the archegonia are protected by the incurved edges of the short female branch, and the young sporogonium by the thick calyptra. Little can be inferred from these different arrangements, beyond the generalisation that while a short collar-like outgrowth, or a circle of

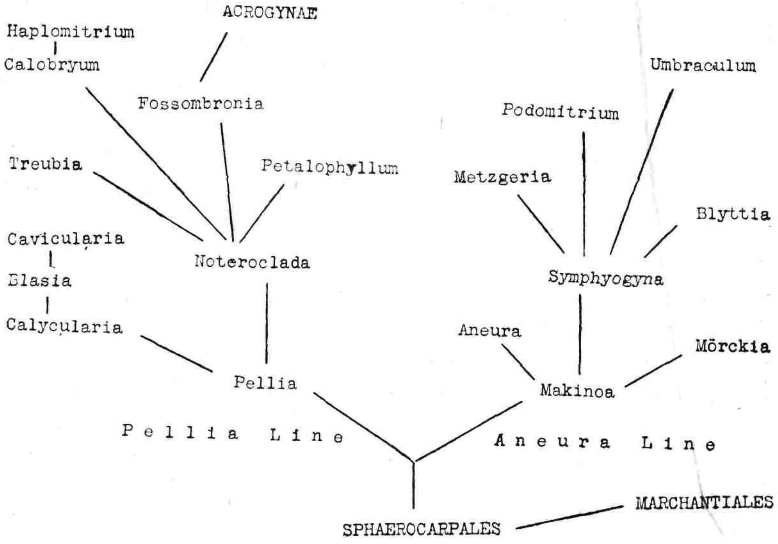
scales, or a single scale, or the inturned and fringed edges of the female branch, suffices for the protection of the archegonia (by forming capillary water-holding spaces), the developing sporogonium requires a more complete cylindrical investment which may be provided in the form of a massive calyptra or of a special tubular outgrowth of the surrounding tissue.

The thick calyptra on the one hand, and the tubular perianth on the other, have apparently arisen independently in several lines of development; we meet with both in genera belonging to the other groups—the perianth in *Calycularia*, *Noteroclada*, *Fossombronia*, and *Petalophyllum*, and the massive calyptra in *Treubia* and the Calobryaceæ. In all the foliose Codoniaceæ (except *Blasia*), as in the Calobryaceæ, the archegonia are protected by the leaves; in *Blasia* and in *Pellia* they are sunk in a cavity in the axis of the plant-body, and in *Calycularia* there is a cupule-like involucre formed from scales. In all the Codoniaceæ, except *Blasia*, the capsule is spherical, and its wall is provided with fibrous thickenings. In *Fossombronia* and *Petalophyllum*, the capsule-wall breaks up into plates, and there is no trace of an elaterophore, but in the other genera, dehiscence occurs by four valves and there is always a more or less highly developed basal elaterophore. The latter reaches its greatest development in *Pellia* and *Noteroclada*, but in most of the other genera is represented only by isolated fixed elater-like cells at the base of the capsule-cavity.

The Codoniaceæ are sharply marked off from the Blyttiaceæ and Aneuraceæ by the capsule structure, especially by the basal elaterophore. The two latter families should perhaps be merged into one. *Podomitrium* connects the Aneuraceæ with the Blyttiaceæ, having the following characters in common with the genus *Blyttia*: perianth laid down before fertilisation occurs in the archegonial group, and formed by outgrowth of several fringed scales which are carried up to form a tube by basal growth; cells of capsule-wall uniformly thickened, without fibres; elaterophore represented only by an apical pad of thin-walled cells; capsule-wall and elaterophore do not split at the top. In *Umbraculum*, which is frequently joined to *Podomitrium* to form the genus *Hymenophytum*, the perianth is laid down before fertilisation, and arises not from scales but from a ring-like outgrowth; the outer cells of the capsule-wall have fibrous thickenings; the capsule opens by four free valves, the elaterophore splitting into four parts which adhere to the tips of the valves, as in *Aneura* and *Metzgeria*. *Makinoa*, though probably more closely

allied to *Symphyogyna* than to any other genus, resembles *Aneura* in having the antheridia sunk in chambers separated from each other by partitions two cells in thickness, each chamber opening by a pore on the upper surface of the thallus—but the antheridia are not developed on special short branches as they are in *Aneura*. Again, *Calycularia* shows some resemblances to *Mörckia* and *Blyttia*, e.g., in having a cupule-like scaly involucre in addition to a perianth, but in the structure of the sporogonium it agrees closely with the Codoniaceæ.

Although many of these resemblances are doubtless due to the occurrence of parallel developments, we may perhaps regard the Anacrogynæ as having diverged along two lines, which we may call the "*Aneura* line" and the "*Pellia* line," though these two genera have highly specialised sporogonia and are somewhat isolated from the genera with which we have classified them. In the *Aneura* line,



Phylogeny of the Anacrogynæ.

including the Aneuraceæ and Blyttiaceæ, the most characteristic feature is the sterilisation of the central apical portion of the sporogonial tissue to form an incomplete columella or elaterophore; while in the *Pellia* line there is a corresponding basal sterilisation to form an elaterophore which projects upwards into the cavity of the capsule. That the elaterophore reaches its highest development in the genera *Aneura* and *Pellia*, while the vegetative structure of

the plant-body is simpler in these genera than in the other Anacrogynæ, may perhaps be accounted for by the fact that *Pellia* and probably the majority of the species of *Aneura* are more hygrophilous than any of the other Anacrogynæ; the three species of *Pellia*, and the terrestrial species of *Aneura* (the winged species are mostly epiphytic), grow in very wet places, and are often submerged in part. The peculiar gemmæ of *Aneura* strongly recall the zoospores of the green Algæ; "the absence of cilia from these cells, which probably are the last reminiscences of the ciliated gonidia of the aquatic ancestral forms, is to be accounted for by the terrestrial habit of *Aneura*" (Campbell). In dealing with the genus *Monoclea*, it was suggested that the formation of a long seta, in which this genus differs from its allies among the Marchantiales, might be correlated with the extremely hygrophilous habitat. The same explanation may be applied to the presence of the highly developed elaterophore of *Aneura* and *Pellia*; in very moist habitats the possession of an efficient method of spore dispersal would probably be advantageous, and it may be noted that the seta is longer in *Pellia* than in any other Hepaticæ, while in *Aneura* the capsule-valves spring back suddenly and the spores are violently thrown out.

In both of these lines we get numerous parallel developments, especially in the vegetative structure of the plant-body and in the investment of the sporogonium. In *Aneura*, the sexual branches are simply ordinary branches which usually stop growing in length after producing the sexual organs, but frequently (especially in the case of male branches) they resume ordinary vegetative growth afterwards. It may be assumed that the ancestors of the *Aneura* line produced the sexual organs on the upper side of ordinary thallus-branches, and that the arrest of growth which normally occurs in *Aneura* when a branch has produced sexual organs is a later modification. The genus which, though showing sporogonial features peculiar to itself, comes nearest to realising such a type, is *Makinoa*, which has a well developed elaterophore and an antheridial receptacle similar to that of *Aneura*, but developed on the ordinary thallus. *Mörckia* apparently belongs to the *Pellia* and *Makinoa* branch of the *Pellia* line, though its many-layered capsule-wall is peculiar. *Mörckia* stands higher than *Makinoa*, the *Aneura*-like massive calyptra of the latter being replaced functionally by a perianth, outside of which a scaly cupule (involucre) is developed; in *Makinoa* the involucre consists of a single scale. From a *Makinoa*-like form, the *Symphyogyna* branch of the *Aneura* line may

be readily derived, by the differentiation of the thallus into a cylindrical midrib and single-layered wings. This *Symphyogyna* plexus has evidently given rise to *Blyttia*, *Podomitrium*, *Umbraculum*, and *Metzgeria*. Of these four genera, *Blyttia* differs from *Symphyogyna* in little except the development of a tubular perianth, but in the other three the sexual organs are restricted to ventral branches. *Metzgeria* shows the simplest type of sexual branches, but the most highly developed elaterophore; its midrib is slender and lacks the conducting strand present in the other genera of the plexus, and neither perianth nor involucre are developed. *Umbraculum* may be derived from a *Symphyogyna*-like form by the relegation of the sexual organs and the development of a perianth after fertilisation. In *Blyttia* and *Podomitrium*, which have many points of resemblance, the perianth is developed before fertilisation, and outside it there is a cup-like involucre; probably *Podomitrium* bears somewhat the same relation to *Blyttia* that *Umbraculum* bears to *Symphyogyna*. A cup-like involucre and a perianth are also present in *Mörckia*, which further resembles *Blyttia*, *Podomitrium*, *Umbraculum*, and *Symphyogyna*, in having conducting strands, though these are feebly developed. But *Mörckia* does not appear to be closely related to the *Symphyogyna* series, and the same double investment of the sporogonium is found in *Calycularia*, which apparently belongs to the *Pellia* line. It is clear that the *Aneura* line is peculiarly rich in parallel developments, exhibited by the evolution of "dendroid" thallus habit, of conducting strands, of leaves, of specialised sexual branches, and of sporogonial investments (involucre and perianth).

In the *Pellia* line, we may distinguish two diverging branches. One of these leads through *Pellia* and *Calycularia* to the foliose genera *Blasia* and *Cavicularia*. The other leads through *Pellia* to *Noteroclada* and the other typical foliose Codoniaceæ, and probably also to the Calobryaceæ and the Acrogynæ. *Treubia* is an isolated genus, with its peculiar vegetative structure and the investment of the sporogonium by a massive calyptra instead of a perianth. *Fossombronia* is closely allied to *Noteroclada*, but its sporogonium is very like that of *Petalophyllum*, though the vegetative organisation of the latter is peculiar. The Calobryaceæ make a distinct approach to the Acrogynæ, but they appear to form a blindly ending line of development, and it is more probable that the Acrogynæ have arisen from a type like *Noteroclada*.

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IV. ACROGYNOUS JUNGERMANNIALES.

IN the Acrogynæ, the plant-body, or at any rate the portion of it which bears the sexual organs, is differentiated into stem and leaves. In some genera there is a thalloid (*Pteropsiella*, *Metzgeriopsis*) or even filamentous (*Protocephalozia*) phase in the life history of the sexual generation, but even in these cases the sexual organs are borne on leafy shoots. When archegonia are produced, whether on the main axis or on its branches, the apical cell itself is transformed into an archegonium, and the vegetative growth of the axis or branch is terminated. The leaves are developed in spiral succession from a three-sided (rarely two-sided) apical cell, and are arranged in two lateral rows, in addition to which there is often a ventral row of under-leaves, or amphigastria, frequently differing from the lateral ones in size and shape.

The antheridia are borne in the axils of more or less modified leaves—" male bracts " or " perigonial leaves." The archegonia are usually surrounded by a special sheath, the " perianth," which arises as a ring-like outgrowth, when the archegonia are ripe, from the tissue immediately outside the group of archegonia; there is frequently, immediately outside the perianth, an " involucre " consisting of more or less modified leaves (" female bracts "). The antheridium is usually spherical, with a slender stalk; the archegonium-neck consists of five rows of cells. The sporogonium is always differentiated into seta and capsule. The capsule opens by four valves, and elaters are always associated with the spores.

The vast majority of the genera and species of Hepaticæ belong to this great group, which has a world-wide distribution but is especially developed in the wet forest regions of the tropics. In round numbers, the Acrogynæ include all save some 60 genera and 700 species of the 250 genera and 4,500 species of Hepaticæ which have been described up to the present time. In Britain, there are only some 70 genera and 250 species of Hepaticæ, and of these 50 genera and 200 species belong to the Acrogynæ. These figures show the striking preponderance of the Acrogynæ over the rest of the Hepaticæ; and the poverty in species of the Hepatic flora of Britain, which resembles the North Temperate regions generally in this respect, is shown by the fact that there are several Acrogynous genera with more species than the total number of British Hepaticæ, e.g. *Plagiochila* with over 500 species, *Frullania* with about 350, *Bazzania* with upwards of 300.

Before dealing with the classification and inter-relationships of the Acrogynæ, we may consider the chief morphological characters of the group, with special reference to the wealth of parallel developments which is one of its most striking features.

The size of the plant varies considerably in the Acrogynæ. Some of the epiphytic Lejeuneas, which grow on living leaves of ferns and flowering-plants, are only a few millimetres long and consist of delicate thin-walled cells, while some of the large bark-inhabiting forms of the same group (e.g. *Bryopteris*) reach a length of several feet and are firm and hard in texture. In his travels on the Amazon, Spruce found remarkable pendent festoons of epiphytic Frullanias, which often formed an important feature in the vegetation of wet tropical forests and which were too thick for a man's arms to surround them.

In the Acroygnæ, the apical cell of the shoot (Fig. 44) has almost invariably the form of a three-sided pyramid, from which three sets of segments are cut off. One side of the apical cell is parallel with the ventral surface of the stem, and the other two sides meet in the middle line above, hence one set of segments is ventral and the other two sets dorso-lateral. From each of the latter a leaf is formed, while the ventral segment may or may not produce an underleaf (amphigastrium). The form of the apical cell is directly related to the size of the underleaf as compared with the lateral leaves. Where the underleaves are well-developed, the three sets of segments are about equal in size, and the apical cell forms in surface view an equilateral triangle; where no underleaves

are formed, the ventral segments are narrow, the apical cell appearing in surface view as an isosceles triangle with a narrow base. In the thalloid vegetative portion of the plant-body in *Metzgeriopsis*, and in the leafy shoot of *Pleurozia* and *Arachniopsis*, however, the apical cell is two-sided, and there are of course only two (lateral) sets of segments.

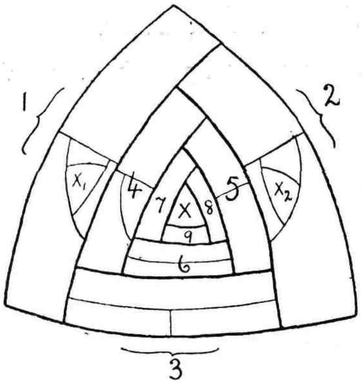


Fig. 44. Diagram of the apical growing-point, seen from the front. X, is the apical cell of the main axis; the last nine segments cut from it are numbered; X_1, X_2, are the apical cells of branches.

Each lateral segment of the apical cell divides first by a radial wall into an upper and a lower cell. This wall may be nearer either the upper or the lower side of the segment, and from the larger of the two cells an inner cell is next cut off which contributes to the formation of the stem, while the two outer cells (upper and lower) give rise to the young leaf. Even when the mature leaf shows no trace of lobing, the very young leaf is distinctly two-lobed, each lobe bearing a mucilage-papilla. In fact, the ultimate form of the leaf depends on the further development of the originally similar and separate upper and lower lobes of the very young leaf. In species with entire leaves, the two lobes grow together (*i.e.* are carried up by common growth at the base) from the first; whereas in forms with divided leaves the lobes grow out independently for a shorter or longer time. The growth of the leaf is at first apical, segments being cut from the terminal cells by transverse walls. When *only* transverse divisions occur in the two primary cells, we get a leaf consisting of two diverging rows of cells (*Arachniopsis*). From these considerations, it is easy to account for the extraordinary variety in form of the mature leaf which is met among the Acrogynæ and which contrasts strongly with the remarkable uniformity of the Moss leaf—the leaves of Mosse sare never lobed,

though the margin may be slightly toothed. The leaves are at first inserted transversely on the stem, and the insertion remains as a transverse line when the leaf consists of two or more simple cell-rows (*Arachniopsis*, *Blepharostoma*), but as a rule the insertion line becomes shifted so that it runs obliquely across the stem. This shifting is due to unequal growth in length of the upper and lower portions of the stem tissue. If this growth is *hypotropic* (greater on the lower side), the stem curves upwards, away from the substratum, at the growing tip of the shoot, the line of insertion

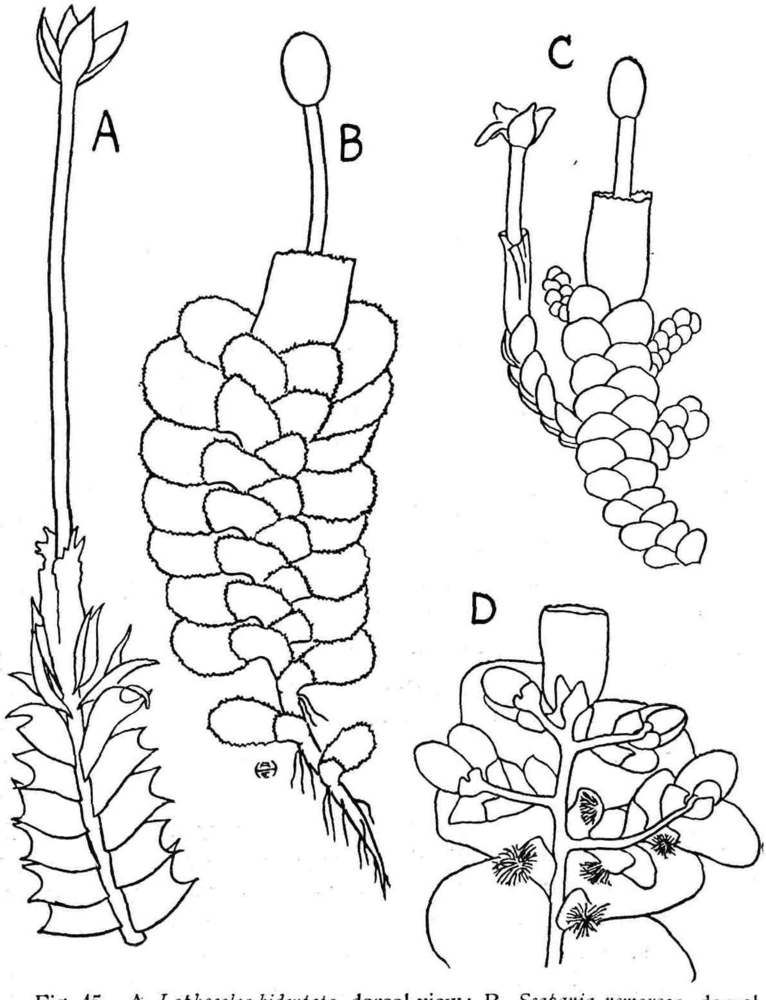


Fig. 45. A, *Lophocolea bidentata*, dorsal view; B, *Scapania nemorosa*, dorsal view; C, *Radula complanata*, dorsal view; D, *Radula*, ventral view. Descriptions of leaf-insertion, leaf-lobing, and perianth are given in the text.

runs forwards and downwards, and the fore edge of the leaf is overlapped by the hinder edge of the next leaf in front—this is the *succubous* arrangement (Fig. 45, A. B). If the growth of the stem is *epitropic* (greater on the upper side), we get the reverse or *incubous* arrangement (Fig. 45, C; Fig. 46).

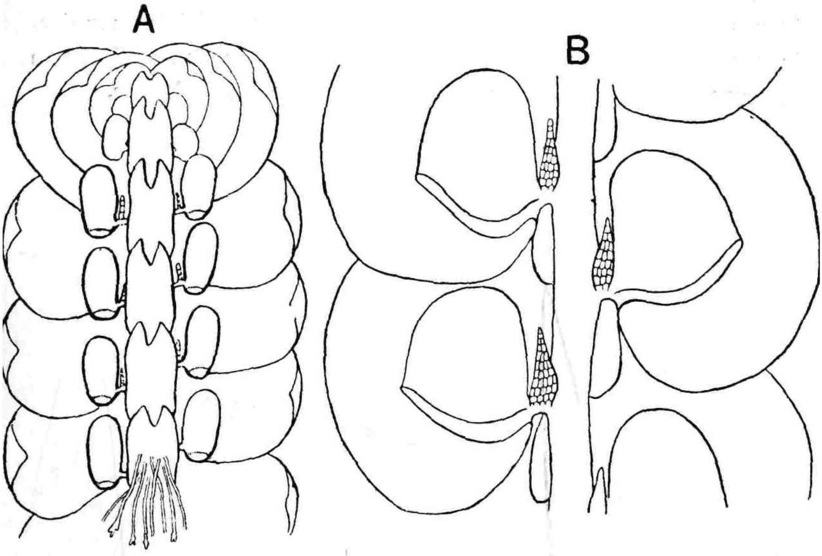


Fig. 46. Leaf-pitchers of *Frullania*, as seen on ventral side of the shoot of (A) *F. tamarisci* and (B) *F. dilatata*.

Taking first the forms in which the leaf is flattened in one plane, the insertion being a straight or slightly curved line, we find every transition between leaves which are entire or very slightly notched and those which are divided to the base into two or more lobes. With this type of insertion, which may be either succubous or incubous, the lobes in the case of notched or divided leaves are usually equal in size. The form of the leaf is, however, often complicated when the lobing is accompanied by folding, each lobe being attached independently to the stem and the two lines of attachment meeting at an angle which is often very sharp, while the leaf itself shows a more or less acute fold or keel. In these "complicate-bilobed" leaves the lobes may be about equal in size (e.g., *Marsupella*, some species of *Scapania*) and the leaf is neither incubous nor succubous. But in most cases the lobes of the complicate leaf are unequal in size, the dorsal lobe being the larger as a rule and the leaf arrangement incubous (e.g., *Radula*, *Porella*,

Frullania), though sometimes the ventral lobe is the larger and the leaves succubous (*Diplophyllum*, most species of *Scapania*). In some cases, the leaves are "fused" in pairs across the dorsal side of the stem (*e.g.*, some species of *Calypogeia*); in others, the leaves are not only united dorsally but their lower margins are continuous with the sides of the underleaf that stands between each pair of leaves (*Arnellia*, *Southbya*); while in *Syzygiella*, which has no under-leaves, the leaves are joined both above and below, so that the stem appears to pass through a series of funnel-like double leaves.

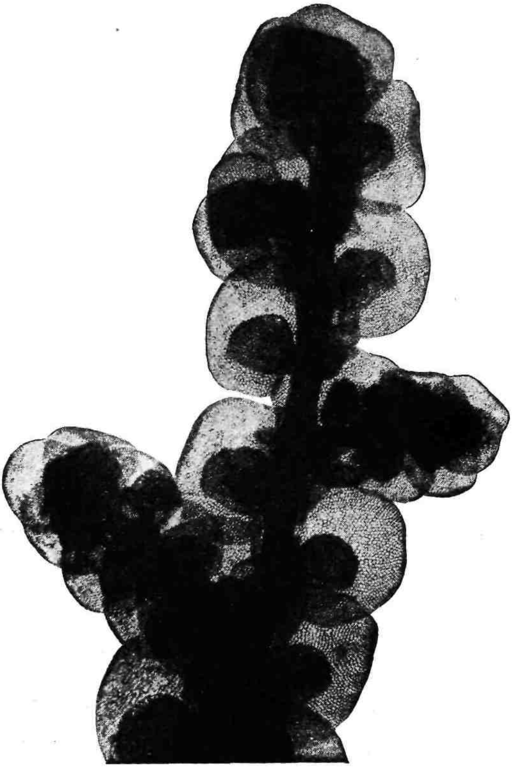


Fig. 47. *Frullania dilatata.*

It is among the forms with folded leaves that we find some of the most remarkable examples of the plasticity of the Acrogynous leaf, mostly serving for the storage of water in various ways. In *Mytilopsis*, the leaf is so sharply folded that the two lobes lie almost parallel, like the valves of a mussel shell open anteriorly by a narrow slit, while the sharp keel bears a narrow wing. In *Micropterygium*, *Gottschea*, etc., the leaf bears a conspicuous wing similar to that found in the Moss-genus *Fissidens*—in *G. ciliata*

there are two wings and the leaf is H-shaped in cross-section. In several genera, belonging to different families, we find *paraphylls*—leaf-like or filamentous outgrowths arising from the stem between, and in addition to, the ordinary leaves; in the curious genus *Stephaniella*, the leaves soon lose their chlorophyll and then serve as transparent scales covering the dense mantle of green filamentous paraphylls with which the stem is clad. Perhaps the most beautiful of these modifications, however, are the *water-sacs* or pitchers, formed by the infolding of either the entire leaf, or the large upper

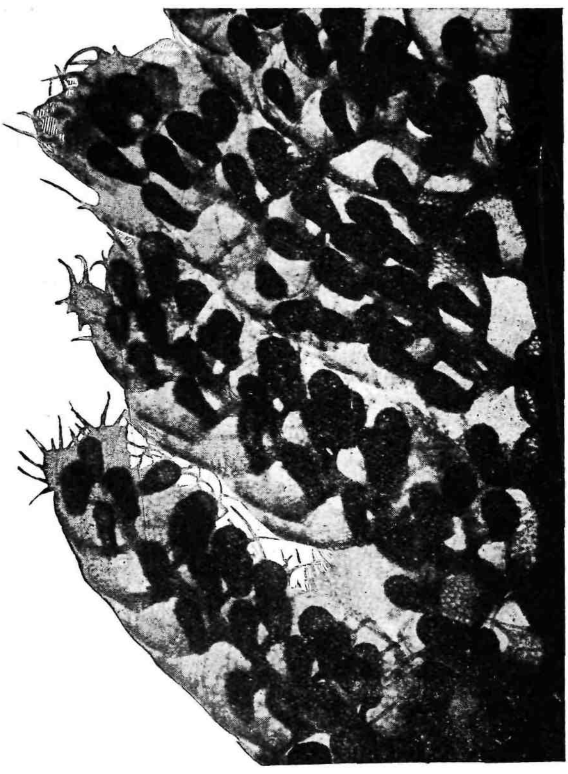


Fig. 48. *Polyotus magellanicus.* Part of a plant showing lower surface of four of the ultimate branches, with numerous water-sacs.

lobe, or, more commonly, the small ventral lobe. Sometimes the pitchers are provided with a valve or trap-door like that of the Bladderwort pitcher. The small ventral-lobe pitchers of *Frullania* (Figs. 46, 47) are well known, but similar pitchers occur in various genera belonging to different families, and in *Polyotus* (Fig. 48) we get a profusion of pitchers developed not only on the side-leaves but also on the underleaves.

Each of the ventral segments cut from the apical cell divides first by a tangential wall; the inner cell adds to the stem tissue, the further development of the outer cell varies considerably. In the simplest case (e.g., *Lejeunea calcarea*) each of these outer cells simply gives rise to a single row of cells on the underside of the stem, but as a rule a radial division occurs giving two cells placed side by side, then each of these produces a mucilage papilla, and an underleaf is formed. The underleaves show hardly any of the modifications exhibited by the side-leaves, as might be expected from their different position. The side-leaves are turned towards the light, the underleaves are usually appressed to the substratum and cut off from light, hence they are usually smaller and often absent altogether. Frequently, however, the shoot grows more or less erect and the underleaves may be equal in size to the side-leaves, the shoot showing practically radial symmetry.

In striking contrast to the varied external morphology of the shoot in the Acrogynæ, we find practically an entire absence of histological differentiation in the stem and leaves. The tissue of the stem is generally quite uniform; though the inner cells may have thinner walls than the outer cells, we rarely find anything approaching even the simple type of conducting strand found in so many Mosses, much less the elaborate differentiation seen in the Polytrichaceæ, etc. In some of the Lejeuneas and Frullanias. certain cells of the leaf are much larger than the others, these "ocelli" being either scattered or arranged in a median line running up the leaf. In a few forms (e.g., *Herberta, Diplophyllum*) there is a "midrib" consisting of a band of elongated cells, which as shown by Tansley (83) serve for conduction. The leaf is rarely more than one cell thick, though in some cases (species of *Gottschea*, etc.) it is several-layered at the base and for some distance upwards. The rhizoids are typically unicellular and unbranched, or slightly branched at the ends, though Goebel (33) notes in *Gottschea* the occurrence of numerous septa in the distal branched portion of the rhizoids.

Various features of interest in the vegetative organs of the Acrogynæ are described by Goebel (32). For an account of asexual reproduction as exhibited in this group, reference may be made to a paper published in this Journal (5).

The distribution of the sexual organs varies greatly, but the commonest condition is that in which the antheridia and archegonia are borne on the same plant but in separate groups or "flowers."

The antheridia (Fig. 52, B, C), which are spherical or ovoid with a slender stalk, are borne in the axils of more or less modified "male bracts" (perigonial leaves), either singly or in groups of from two to about twelve; they are sometimes (*Scapania*, etc.) accompanied by filamentous or narrow leaf-like paraphyses. The perigonial leaves are always simple and symmetrical in form, even in species where the ordinary leaves are deeply divided into lobes differing greatly in size and shape and show other modifications (water-sacs, etc.). The antheridia are seldom borne in the axils of the under-leaves where these are present, and they are often produced on special short catkin-like branches, the "male bracts" being crowded and often having saccate bases for the better protection of, and especially the retention of moisture about, the antheridia.

The archegonia are borne in terminal groups at the apex of the main axis, or of its ordinary branches, or of special short branches —the latter often arising from the underside of the stem. In any case, the development of an archegonial group—probably that of the first archegonium in the group—uses up the apical cell and thus terminates the growth of the stem. In the Lejeuneas a single archegonium is developed, and in *Frullania* (Fig. 52, D, E) only two or three, but in most cases the group contains a large number (sometimes a hundred or more) though as a rule a single mature sporogonium is produced. The archegonial group is surrounded by an "involucre" or "perichætium" consisting of leaves which usually differ in their larger size and in other respects from the ordinary vegetative leaves. The archegonial branch generally tends to grow erect, and the underleaves ("bracteoles") of the "involucre" are then nearly or quite as large as the leaves ("bracts") and are usually present even in species which lack underleaves on the rest of the shoot. The bracts are often more extensively laciniated and fringed than the vegetative leaves, as an adaptation for retaining moisture by capillarity, but on the whole they are, throughout the Acrogynæ, less specialised than the leaves. For instance, they are usually divided symmetrically by a median notch of greater or less depth, alike in species with entire rounded leaves and in those with the leaves cleft into a larger and a smaller lobe, and they never show special structures like water-sacs.

In the great majority of Acrogynæ, the archegonial group becomes surrounded by a tubular organ—the "perianth"—which arises within the involucre, making its appearance after the development of the archegonia themselves. As a rule, the formation

of this organ occurs independently of fertilisation, though it probably does not reach mature size if no archegonia have been fertilised. The perianth is by most writers regarded as a structure formed by the fusion of the uppermost leaves (two or three in number according to the species) of the female axis. In many cases, the form of the mature perianth certainly supports the view that it corresponds to concrescent leaves, the orientation of which agrees with that of the ordinary vegetative leaves of the species. The union of two leaves and an underleaf, all remaining flat, gives a perianth of the "epigonanthous" type, having the form of a triangular prism, three angles or keels being formed by the united margins of the leaves; one of the flat sides is ventral, one of the keels dorsal—e.g., *Lophocolea* (Fig. 49, A). A modification of this is seen when no under-leaf takes part in the formation of the perianth—the latter is compressed laterally—e.g., *Plagiochila* (Fig. 49, B). When the

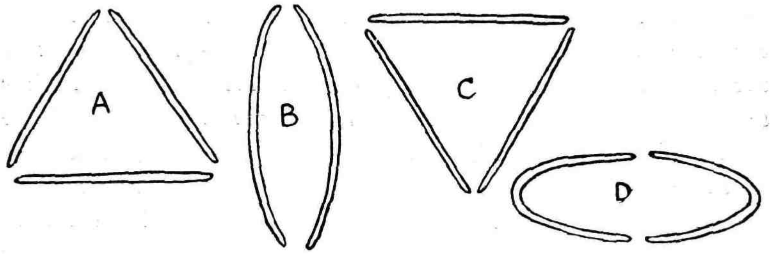


Fig. 49. Diagrammatic transverse sections of four types of perianth in Acrogynæ. A, is epigonanthous; C, hypogonanthous; B, compressed laterally; D, compressed dorso-ventrally.

perianth-forming leaves are folded, instead of being flat, we may again get a triangular perianth, but this time the third keel is ventral instead of dorsal; this "hypogonanthous" type (Fig. 49, C) occurs in many genera, e.g., *Cephalozia*, *Bazzania*, *Lepidozia*, *Porella*, *Frullania*, and the Lejeuneas. When no under-leaf enters into this type of perianth, we again have a compressed structure, but this time (Fig. 49, D) the flattening is dorsiventral—parallel with the substratum instead of at right angles to it (e.g., *Scapania*, *Radula*). But in many species the form of the perianth does not fall into line with these types, and if we support the interpretation that the perianth is invariably a foliar structure, it is not easy to account for the many cases in which it is devoid entirely of angles or keels; in other cases the interpretation is made difficult by the presence of additional keels, which may be without any definite orientation. According to Leitgeb (54) the perianth arises from the last segments cut from the apical cell before the latter becomes used up in the

formation of the archegonia. We have seen that vegetative leaves may undergo concrescence, and in some cases this occurs with the leaves (bracts) of the involucre. The perianth may be absent altogether—a condition especially found in species having a fruit-sac or marsupium.

In its fully-developed form, the marsupium is a tubular structure which grows downwards into the substratum, bearing rhizoids on its outer surface, while the young sporogonium develops inside it at the closed lower end, and the ripe capsule is thrust out of its open upper end when the seta elongates. The development of the marsupium has been investigated by Gottsche (34, 35) and by Leitgeb (57), and more recently by Goebel (32, 33) and by Douin (7). All the species possessing this remarkable structure were until recently classed together as an independent family, the "Geocalyceæ," but this is an entirely artificial group, the marsupial genera and species being scattered over four of the eight families of Acrogynæ now generally recognised. The independent origin of the marsupium in unrelated genera, and in certain species of otherwise normal genera, forms one of the most striking examples of homoplasy to be found even in the Hepaticæ. Moreover, the marsupium has clearly arisen in several different ways in different cases, as we shall presently see.

The whole subject of the arrangements for the protection and nutrition of the developing sporogonium has never received the detailed consideration which it deserves, though these arrangements appear to be of great importance in connexion with the phylogeny of the Acrogynæ. In the simplest case, typical of the majority of the Acrogynous genera, the young sporogonium is invested by (1) the calyptra formed from the venter of the fertilised archegonium, (2) the perianth, which arises as a ring-like outgrowth around the archegonial group, and which is doubtfully regarded as a concrescent leaf structure, and (3) the involucre of more or less modified leaves —all these envelopes being free from each other, while the foot, or enlarged base of the sporogonial seta, is embedded in the base of the calyptra (Fig. 50, I.).

The writer has investigated the morphology of the sporogonial envelopes in species belonging to the majority of the genera of Acrogynæ, and has found that in nearly half of the genera (excluding the Lejeuneaceæ), there are indications of stages leading up to the fully developed marsupium of the "Geocalyceæ." Starting from the simplest condition in which the three envelopes—calyptra,

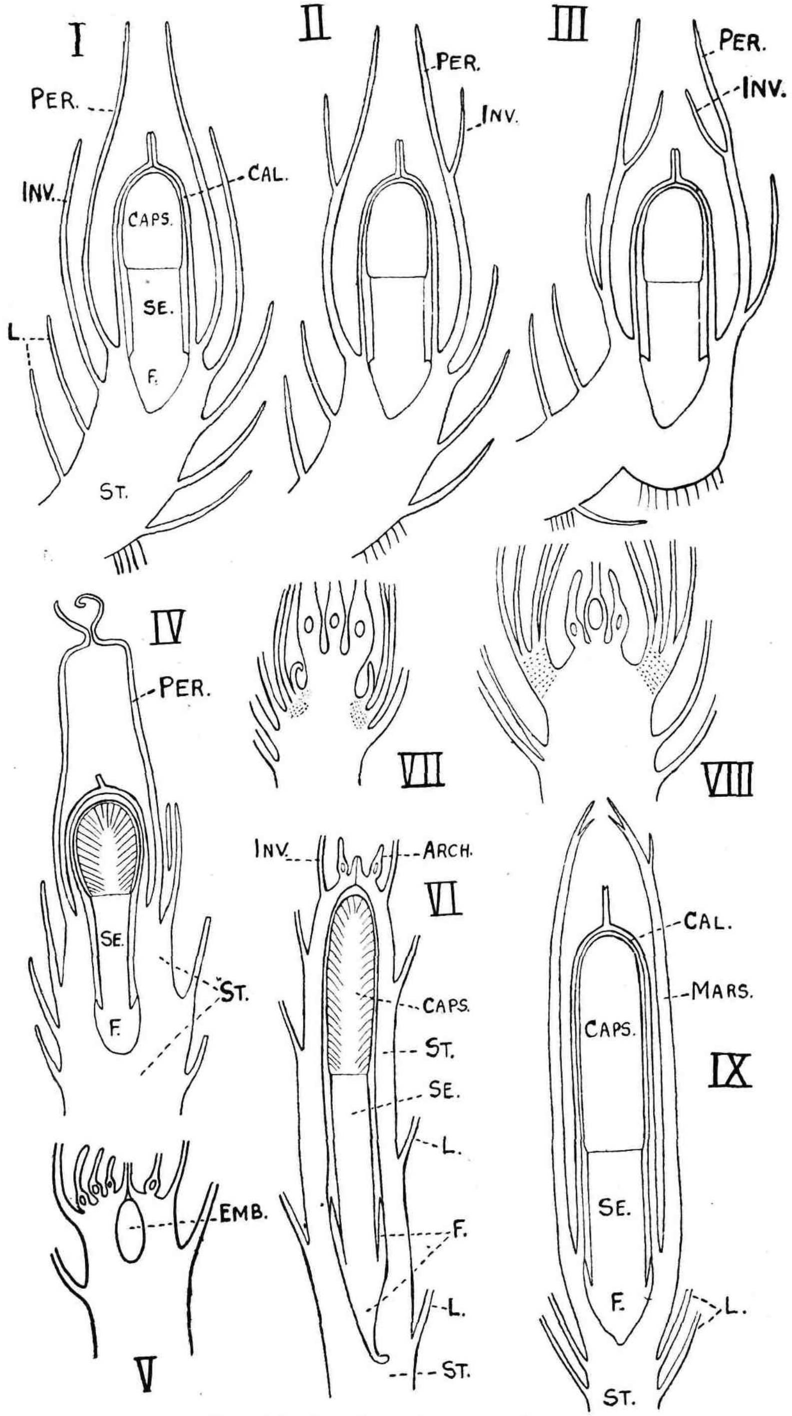


Fig. 50.—*For description see next page.*

Fig. 50. Diagrammatic longitudinal sections of various Acrogynæ, showing the archegonial group and the sporogonium with the structures developed around them. I.—Perianth and involucre free (e.g., *Lophocolea, Plagiochila, Frullania*). II.—Perianth and involucre "fused"—*i.e.*, carried up by the growth of a basal ring-like zone of stem tissue (e.g., *Eucalyx*). III.—Perianth and involucre "fused"; the formation of an incipient marsupium ("fruit-sac") indicated by the bulbous swelling of the stem below the foot of the sporogonium (e.g., *Nardia geoscypha*) IV.—The seta and foot of the sporogonium have penetrated for some depth into the stem tissue (e.g., *Cephalozia bicuspidata*). V. and VI.—Two stages in the development of "cœlocauly"—the complete embedding of the sporogonium in the stem tissue e.g., *Gottschea, Trichocolea*). VII. to IX.—Three stages in the development of the erect marsupium of *Isotachis*. Arch., archegonia; cal., calyptra; caps., capsule; emb., embryo sporophyte; f., foot; inv., involucre; l., leaf; mars., marsupium; per., perianth; se., seta; st., stem. Figures IV. to IX. are from Goebel.

perianth, involucre—are free from each other and the sporogonium foot extends only to about the insertion of the involucre, we may trace various lines of specialisation, resulting in the more complete investment of the young sporogonium, and culminating in the various types of fruit-sac which can be distinguished among the marsupial Acrogynæ.

Among the various processes which tend to facilitate the nursing of the young sporogonium, and of which several may take place hand in hand, the simplest is the following. The seta, capped by the absorbing foot or haustorium, grows actively downwards into the stem tissue, which may either remain unaltered or may grow in thickness so as to form a thick protective and food-storing sheath around it. In many cases, the foot penetrates below the insertion of the involucre, so that only the capsule and upper part of the seta of the ripe, but not yet exserted, sporogonium are covered by the calyptra, but no further special development occurs (Fig. 50, IV.). In other cases, however, the portion of stem underlying the archegonial group grows actively, in such a way that more and more of the lower portion of the sporogonium becomes sunken in it and surrounded by a thick sheath formed of stem tissue, while the calyptra gradually dwindles in size. In *Leiomitra*, the calyptra is still recognisable as a thin envelope covering the capsule itself. In the allied genera *Trichocolea* and *Polyotus*, there is no calyptra at all, if we limit the idea of a calyptra to the result of growth of the archegonium venter; the so-called "calyptra" is here in reality formed from the stem tissue, into which the lower end of the sporogonium burrows deeply, and which bears at the apex the unfertilised archegonia (and the neck of the fertilised one), while the involucral leaves are either carried up on its sides or form a crown at the top (Fig. 50, V., VI.). In the three genera just

mentioned, there is no perianth, and the same is true of practically all the forms with a well-developed marsupium.

In a considerable number of genera, belonging to different families, we find a series of changes which lead up to the formation of a distinctly sac-like structure, arising after fertilisation from the tissue of the stem and resulting in the development of a definite and conspicuous marsupium. Three main types may be distinguished.

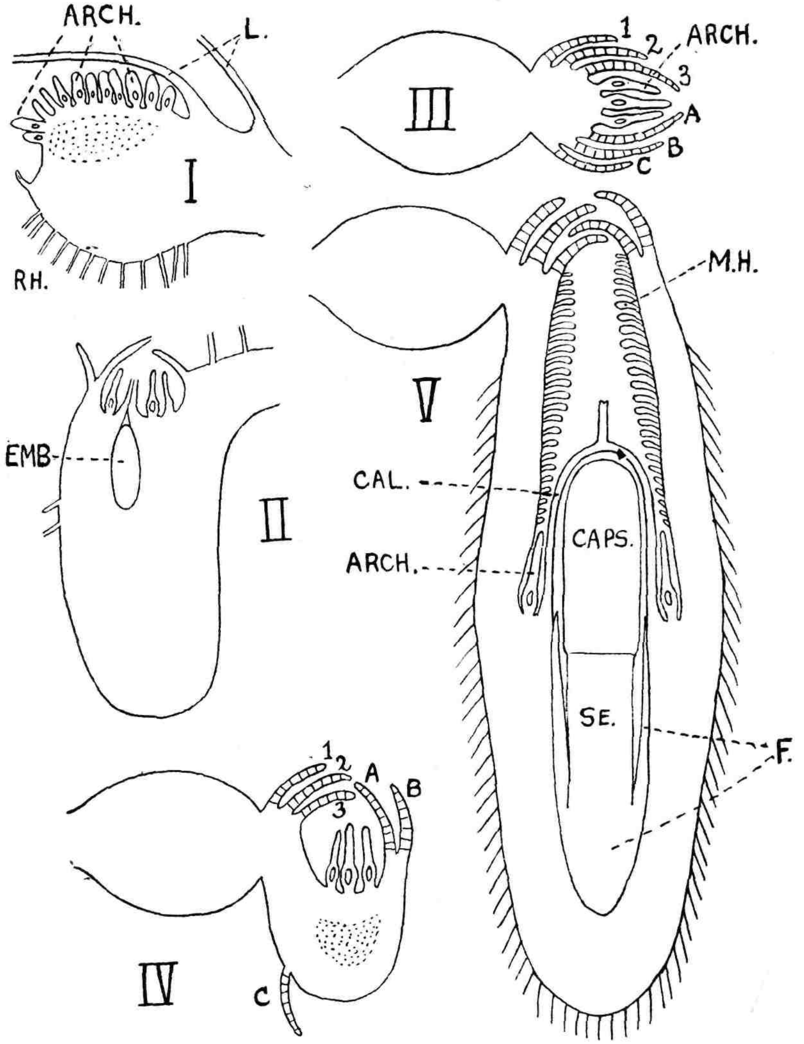


Fig. 51. Stages in the development of the solid marsupium of *Tylimanthus* (I., II.) and of the hollow marsupium of *Kantia trichomanis* (III. to V.) Lettering as in Fig. 44; rh., rhizoids. All except V. from Goebel.

(1) The *Isotachis* type, in which the symmetry of the shoot remains unchanged, and the sac-forming meristem arises as a ring-like outgrowth of the stem tissue around the archegonial group (Fig. 50, VII. to IX.). (2) The *Tylimanthus* type, in which the sac-forming meristem is at first a solid mass of tissue, which grows at right angles to the long axis of the stem itself, and which invests and is penetrated by the embryo (Fig. 51, I., II.). (3) The *Acrobolbus* type, in which the meristem arises as a *hollow* ventral outgrowth from the archegonial branch (Fig. 51, III. to V.).

The origin of the *Isotachis* type of marsupium, in which the latter forms a direct linear continuation of the archegonium-bearing axis, may be traced in certain species described by systematists as having the perianth and involucre "fused" or concrescent. The "fusion" is brought about by the growth of a ring-like zone of tissue at the base of the perianth and involucre, both of which are carried up on a collar or tube (Fig. 50, II.) This process reaches different stages in different genera, e.g., *Nardia*, *Marsupella*, *Southbya*, and is most striking in *Isotachis*. Here the archegonial branch grows erect, and the stem-tissue grows up to form a long thick envelope which carries up with it the involucral and neighbouring leaves, as shown by Goebel (33). We thus get in *Isotachis* what looks like a perianth and has usually been described as one, but is really a marsupium. In the marsupia of the *Tylimanthus* and *Acrobolbus* types, the solid or tubular tissue-zone which produces the marsupium grows downwards, making a right angle with the axis of the plant and usually becoming attached by rhizoids to the substratum, into which it may burrow to some depth.

The beginnings of these different types of marsupium may be traced among certain species of *Nardia*. The case of *N. geoscypha* is specially interesting. Here the plant may either grow erect or horizontally. In the former case, the cup-like outgrowth which after fertilisation carries up the perianth and involucre, as already described, grows upwards and the developing sporogonium is parallel with the axis of the plant. In creeping plants, however, the ventral tissue of the stem grows so as to form a solid mass below the archegonial group; this swelling projects below and bears rhizoids, and its tissue contains food for the nutrition of the developing sporogonium, the absorbing organ (foot) of which becomes buried in the swelling (Fig. 50, III.) Thus in this species we have the beginnings of both the *Isotachis* and the *Tylimanthus* types of marsupium. The ventral form of incipient marsupium is

found also in some other species of *Nardia* and in *Notoscyphus*, *Gyrothyra*, *Prasanthus*, and a few other genera. In these forms a perianth is usually still present, but it disappears in *Prasanthus*, and it rarely occurs in the more fully developed marsupia—obviously because it is no longer required, the protection of the sporogonium being taken over by the marsupium itself. The highest development of the solid type of ventral marsupium is found in the genera *Tylimanthus*, *Marsupidium*, and *Marsupellopsis*.

In the *Acrobolbus* type, which includes the majority of the marsupial Acrogynæ, the marsupium is tubular from the beginning, as compared with the solid *Tylimanthus* type, but transitions occur between the two types. In the *Tylimanthus* type the archegonial group shows dorsiventral symmetry, the archegonia being developed only on the dorsal side of the stem, and the marsupium is formed by active growth of the underlying tissue. In the *Isotachis* type the archegonial group shows radial symmetry, the archegonia being produced all round the apex of the erect stem, and the marsupium arises as a ring-like outgrowth of the stem-tissue. In the development of the *Acrobolbus* type, we have a combination of the conditions seen in the *Tylimanthus* and *Isotachis* types. The archegonial group is either developed on the upper half of the stem to begin with, or is displaced to the upper side by the growth of the ventral tissue. In either case, after fertilisation has occurred, this ventral tissue grows downwards, forming a cup which becomes extended to produce a tube, into the thickened lower end of which the sporogonial foot is plunged. In *Arnellia*, the marsupium begins in much the same way as in *Nardia geoscypha*, but the ventral swelling formed at the end of the archegonial branch becomes a shallow cup, to the bottom of which the archegonial group is carried, the calyptra remaining free right to the base of the cup, while the perianth and involucre are left at the mouth; growth is soon arrested, and the marsupium remains in this incipient stage. In *Harpanthus*, a similar cup-like marsupium is formed, but the calyptra is adnate to the inner surface of the cup; in *Adelanthus*, both calyptra and perianth are carried down into the short marsupium. Finally, in the genera *Acrobolbus*, *Calypogeia*, *Lethocolea*, *Symphyomitra*, *Kantia*, *Saccogyna*, and *Balantiopsis*, we get well-developed tubular marsupia, sometimes reaching a length of several centimetres and completely investing the mature sporogonium. In some cases the meristem at the base of the developing marsupium is covered by inactive tissue which, as Goebel has pointed out, resembles a root-cap in structure and

behaviour. The interior of the marsupium is frequently lined by outgrowths bearing papillæ which secrete a gummy liquid (Fig. 51, V.), and the wall of the marsupium may be strengthened by a network of thick-walled cells.

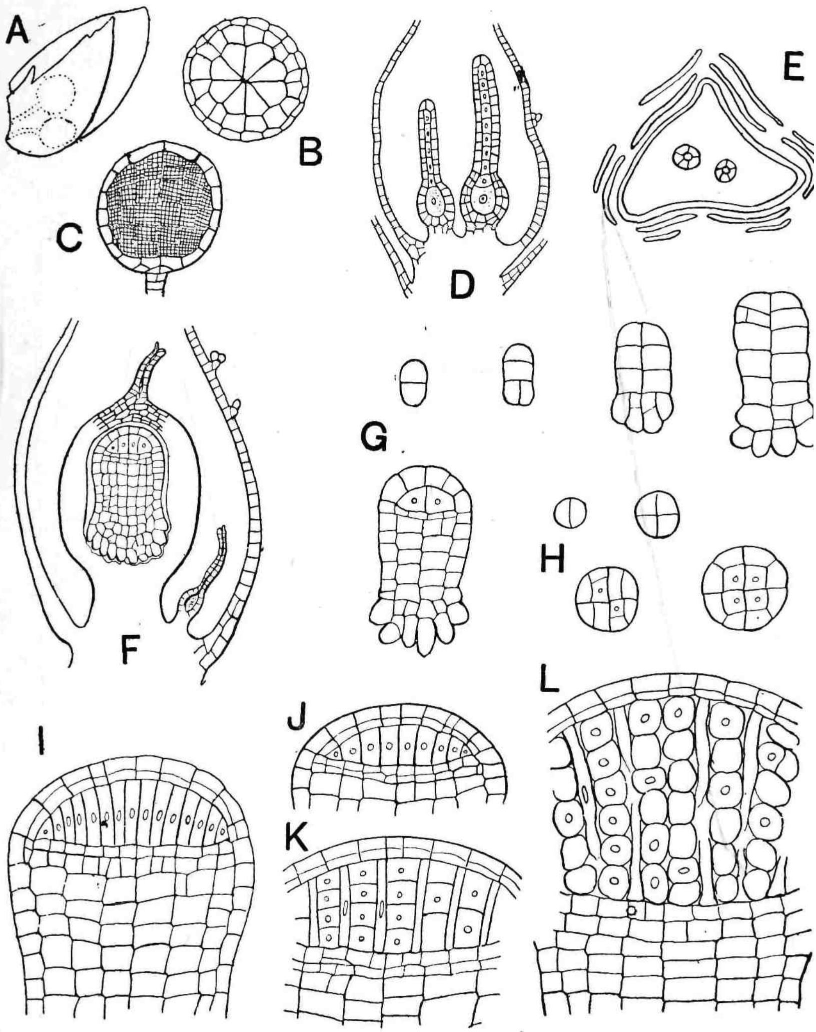


Fig. 52. *Frullania dilatata.* A, a perigonial leaf (male bract), from ventral surface, showing two antheridia; B, C, antheridium in apical view and in longitudinal section; D, longitudinal section of perianth with two archegonia; E, transverse section of same; F, longitudinal section of perianth showing embryo in fertilised archegonium, with unfertilised archegonium on the right; G, a series of longitudinal, and H, a series of transverse sections of embryos of different ages; I, J, K, L, longitudinal sections of older sporogonia, to show development of spores and elaters.

The Lejeuneaceæ, including *Frullania*, *Jubula*, and the Lejeuneæ, are sharply marked off from the remaining Acrogynæ in the structure and development of the sporogonium. The embryology of *Frullania* has been described and figured more completely than that of any other genus of Acrogynæ, having been investigated by Kienitz-Gerloff (49), Leitgeb (54), Leclerc du Sablon (52), and the writer (6). The first wall is transverse, the lower (hypobasal) cell then divides by a vertical wall and the upper (epibasal) cell by a transverse wall (Fig. 52, G). Each of the two upper cells then divides by two sets of vertical walls intersecting at right angles; meanwhile the two hypobasal cells also divide again by vertical walls, so that the embryo consists of three tiers, each with four cells. The hypobasal cells soon project and divide somewhat irregularly to form the blunt foot or haustorium which presses into the tissue forming the stalk of the archegonium. The cells of the uppermost tier divide by tangential walls into four inner cells (archesporium) with denser protoplasm than the four outer cells which form the capsule-wall. The middle tier divides by longitudinal walls separating eight outer cells from four inner ones; this tier produces the stalk and lower part of the capsule. The divisions in the four primary archesporial cells are extraordinarily regular and diagrammatic. At first only longitudinal divisions occur, until there is formed a lens-like mass of about two hundred cells, the central cells being longer than the outer ones (Fig. 52, I, J). These cells then become differentiated into two sets. Some divide transversely to form rows of spore-mother-cells; the others grow in length but remain undivided, forming long cylindrical cells attached to the inner surface of the capsule-wall above, and to the floor of the capsule below. The rows of cubical sporogenous cells alternate regularly with the long undivided cells, each of which will form an elater extending the entire depth of the capsule (Fig. 53, A). Each elater becomes flattened and trumpet-like at the lower end, and contains a single broad spiral band; there are about a hundred of them in a well-grown *Frullania* capsule, those nearest the centre being the longest. The structure of the two-layered capsule-wall is very characteristic: the cells of the outer layer have rod-like fibres on their lateral walls, especially at the angles between adjacent cells, while on the walls of the inner layer the thickenings form an irregular net work (Fig. 53, D). The seta is not so sharply marked off from the capsule as in most liverworts, for at the base of the capsule there is a mass of thin-walled tissue corresponding to the apophysis

of a moss sporogonium, hence at dehiscence the four valves of the capsule do not become free right down to the point of junction with the cylindrical seta ; in systematic books the capsule of *Frullania* is therefore described as "opening for only two-thirds of its length." When the ripe capsule dries, the elaters contract and their lower ends become free from the floor of the capsule while their more

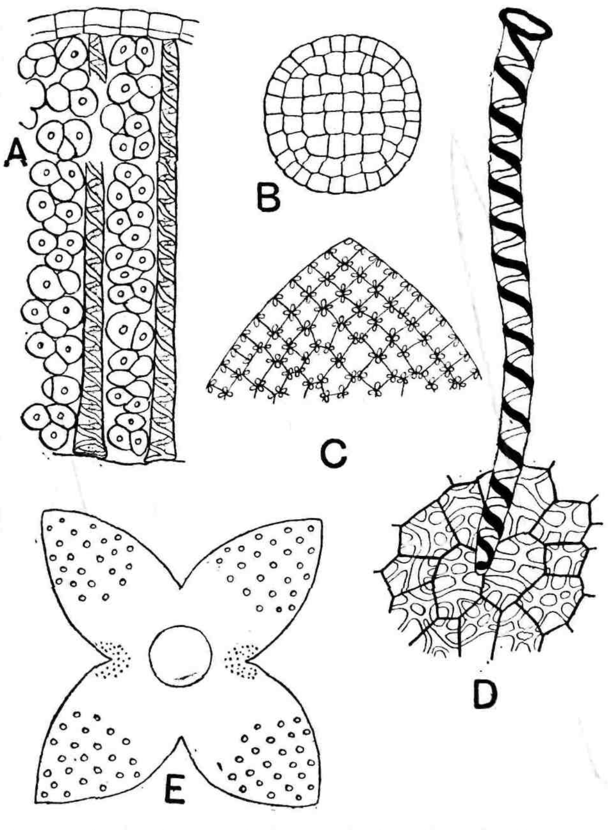


Fig. 53. *Frullania dilatata.* A, longitudinal section of well-grown capsule, with spore-mother cells dividing ; B, cross section of seta ; C, part of wall of capsule (upper end of one of the four valves) seen from outer surface ; D, part of inner surface of capsule-wall, with an elater ; E, diagram (from Jack, 'Bot. Zeit.,' 1877) showing the arrangement of the elaters on the four valves of the capsule-wall, as seen from above.

firmly fixed upper ends remain attached to the inner surface of the capsule-wall. Then the wall splits from above downwards into four valves (Fig. 54) which spring outwards with explosive violence, the spores being flicked away to a distance of several inches by the sling-like action of the elaters which are suddenly bent outwards with the four valves.

In the remaining Acrogynæ, the elaters and spores never show the same relation to each other as in the Lejeuneaceæ, and frequently they are mingled quite irregularly. In many cases, however, they show a tendency to radiate from the base when the capsule is spherical, and to be arranged more or less horizontally around a central longitudinal axis when the capsule is oblong in form. In *Lepicolea*, most of the elaters are of the normal bi-spiral type and mingled with the spores, but from the base of the capsule there springs a tuft of much larger fixed elaters having a single spiral fibre; this exactly corresponds to the elaterophore of *Pellia* in both

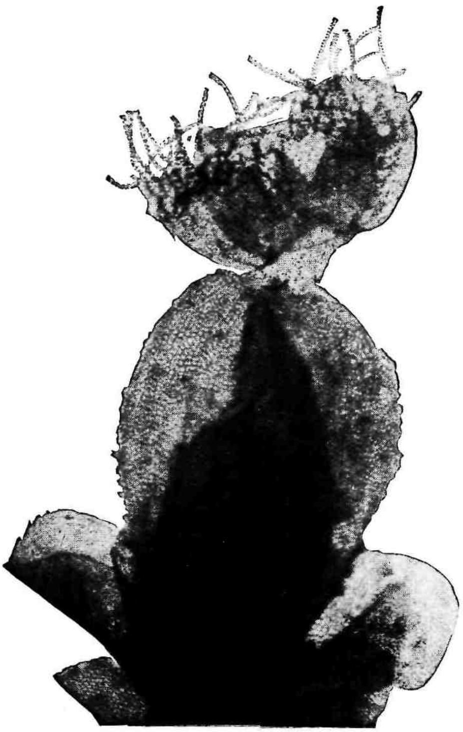


Fig. 54. *Frullania dilatata.* End of a female branch (dorsal view) with capsule, which has exploded and shed the spores, after having (by the elongation of the seta), broken out of the calyptra and the perianth. The calyptra, bearing the withered archegonium-neck, can be seen inside the perianth; the tubercles on the outer surface of the perianth are plainly shown on either side.

position and structure. Goebel (33) has recently shown that in *Gottschea splanchnophylla* there is a well-developed rod-like basal columella or elaterophore, corresponding in *structure* with the apical elaterophore of *Aneura* and *Metzgeria*, but resembling in *position* the basal tuft of fixed elaters in *Pellia*. With very few exceptions, the

capsule-wall has well-developed fibrous thickenings in its cells, which are usually arranged in two layers. An apical cap or lens-like thickening of the capsule-wall, such as occurs in many Marchantiales and Anacrogynæ, is apparently never found in Acrogynæ, but the number of layers composing the capsule-wall is often more than two, and may be as many as eight.

The capsule-wall and the seta are remarkably constant in structure in the various genera and groups of genera, thus affording characters of considerable value in classification, and in some cases affording a useful clue to the probable inter-relationships of the orders. For instance the genera *Porella* and *Radula*, forming the two orders Radulaceæ and Porellaceæ, approach the Lejeuneaceæ even more closely in the structure of the capsule-wall than in the vegetative characters which led the older systematists (*e.g.*, in the Synopsis Hepaticarum) to unite these two genera into the tribe "Platyphylleæ" and place this next to the "Jubuleæ" (Lejeuneaceæ). Again, the genus *Pleurozia (Physiotium)* was placed with genera like *Lepidozia* and *Calypogeia* in the "Trichomanoideæ" of the Synopsis, while in Engler and Prantl it is given ordinal rank and brought close to the Lejeuneaceæ. *Pleurozia* differs from *Radula*, *Porella*, and the Lejeuneaceæ in that the capsule-wall consists of about eight instead of two layers of cells, but in other genera with a many-layered capsule-wall all the layers except the outermost one consist of flattened cells, while in *Pleurozia* the innermost layer has precisely the same type of thickening as the inner of the two layers in the Lejeuneaceæ. That is to say, the capsule-wall of *Pleurozia* has evidently been derived from the *Lejeunea* and *Frullania* type by the interpolation of several layers of narrow flat cells between the outer and the inner layer of more or less cubical cells, and the structure of the capsule supports the evidence drawn from other characters as to the probable relationship between *Pleurozia* and the Lejeuneaceæ.

In certain genera of Acrogynæ, the gametophyte shows a remarkable degree of dimorphism, in that the germinating spore produces a vegetative thalloid plant-body on which arise leafy shoots bearing the sexual organs. In two of these genera (*Metzgeriopsis* and *Pteropsiella*) the vegetative body is a flattened thallus resembling that of an *Aneura* or a *Metzgeria*, while in *Protocephalozia* it is a branching filamentous structure closely resembling the protonema of a typical Moss. In each case, the sexual organs are borne on leafy branches which have the typical Acrogynous

characters, and the structure of these branches and of the sporogonium and its envelopes enable us to refer these aberrant genera to their systematic position in the group.

In *Metzgeriopsis* (*Thallolejeunea*) *pusilla*, an epiphyllous plant discovered by Goebel (28) in Java and investigated by him and also by Schiffner (70), the thalloid plant-body is ribbon-like, branched pinnately, and consists of a single layer of cells; each branch grows by a two-sided apical cell, as in *Metzgeria*. Along the margin of the thallus there arise appendages arranged in regular order and consisting of cell-rows; from their regular succession, these appendages may, perhaps, be regarded, as Goebel points out, as rudimentary leaves. The thallus is fixed to the substratum by rhizoids, and it is propagated asexually by gemmæ. The plant is diœcious, and may bear a considerable number of male or female leafy shoots, each of these shoots replacing an ordinary branch. Each sexual shoot grows by a three-sided apical cell, which is doubtless derived directly from the two-sided apical cell of an ordinary branch, and after producing one or two rudimentary leaves it proceeds to the development of large well-developed bilobed leaves which protect the sexual organs. The male catkin-like branches bear about ten perigonial leaves, each saccate at the base and having a pair of antheridia in its axil; the female branch has about six leaves, the largest two forming the involucre around the perianth. At the base of each sexual shoot, rhizoids are usually given off in a tuft.

In *Pteropsiella frondiformis*, discovered by Spruce in Brazil, growing on fallen leaves and decaying wood, the vegetative body is a strap-like thallus which resembles that of *Podomitrium* or the species belonging to the "Repentes" sections of *Blyttia* and *Symphyogyna*, rather than that of *Metzgeria*. It has a well-marked midrib about six cells thick, and on either side an expanded single-layered wing. Growth takes place by a three-sided apical cell, each lateral segment bearing papillæ which come to occupy the margin of the wing at regular intervals, while the ventral segments produce small simple amphigastria. From the midrib, on the lower side of the thallus, there arise sterile thalloid branches and also leafy sexual shoots. The male shoot has a stalk-like base continuous with the midrib of the thallus, and bears numerous male bracts in two lateral rows—the writer (5) has noted that in some cases the male shoot may resume vegetative "thalloid" growth after producing the antheridia, the apex growing out to form a flattened expansion on either side of the mid-rib or stem. The female branch bears a

few involucral leaves in three rows, and finally the archegonial group surrounded by the perianth, these structures agreeing closely with the *Cephalozia* type.

Protocephalozia ephemeroides is closely allied to *Pteropsiella* and placed with it in the Cephaloziaceæ. Spruce, who discovered this curious little plant in Venezuela, growing on moist soil in shade and on mounds thrown up by mud-worms, says "I had already found a minute Phascoid moss (*Ephemerum æquinoctiale*) in simila sites; it is the only *Phascum* known to me that grows on the hot plains of the equator, and at first sight I took the *Protocephalozia* for a second species of the same genus, for I saw on the lumps of mould only a greenish confervoid film, with large perichætia standing out of it here and there—very like the *Ephemerum serratum* on our garden-pots in England. The prothallium of all Cephalozias is narrow and threadlike—very different from the suborbicular prothallium and propagula of *Radula*, *Lejeunea*, and many other Hepaticæ: and it approaches the nearest of any among Hepaticæ to the protonema of true mosses." The vegetative organs consist simply of branching cell-rows, exactly resembling the filamentous protonema of Mosses and differentiated into an underground portion in which the cells have smooth thin walls and no chlorophyll, and an aerial portion which tends to grow erect, is profusely branched, contains chloroplasts, and has the cell-walls covered externally with papillate thickenings. At certain points on this protonema, the branches remain short, develop an apical cell of the usual three-sided type, and give rise to the leafy sexual shoots. The plant has a tufted habit, the usually solitary female shoot arising from the base and the male shoots higher up on the branching filaments.

The classification of the Acrogynæ here suggested is based upon that proposed by Spruce in his classical work on the Hepaticæ of the Amazon and the Andes (78), with some slight alterations.

A. Leaves typically divided into a large upper and a small lower lobe, the latter usually rolled up or saccate; underleaves usually present; perianth usually with wing-like ridges, contracted at the apex to a tubular beak, and ruptured irregularly by the exsertion of the short-stalked capsule; elaters few, with a single spiral fibre, all fixed by their upper ends to the inside of the capsule-wall and extending to the floor of the capsule-cavity; archegonia from one to four (rarely more) in a group.

1.—Lejeuneaceæ. This is the largest family, including nearly 2,000 species of which the majority belong to

the old genus *Lejeunea*, now broken up into about sixty genera. *Frullania*, the sub-genera of which should perhaps be treated as independent genera, is sharply distinguished from the Lejeuneas by its helmet-shaped water-sacs, though the genus *Jubula*, as shown by Evans (16), forms in various respects a connecting link between the Lejeuneas and the Frullanias. The most remarkable of the Lejeuneas is *Metzgeriopsis* (*Thallolejeunea*).

B. Leaves various as to form and insertion; perianth rarely with longitudinal wings; capsule usually long-stalked; elaters numerous and arranged in various ways but never fixed above or extending from roof to floor of capsule-cavity; each elater with two or more spiral fibres; archegonia always more than four, usually numerous, in a group.

a. Leaves typically with two lobes folded upon each other and differing in size and often also in form.

2.—PORELLACEÆ. Lower leaf-lobe small, flat or concave, but never saccate or bearing rhizoids; underleaves present; perianth dorsiventrally compressed; capsule-valves not extending to base of capsule. Only genus *Porella*.

3.—PLEUROZIACEÆ. Upper leaf-lobe larger than lower, the latter saccate and often provided with a trap-door mechanism; underleaves absent; perianth elongated and folded. Only genus *Pleurozia*.

4.—RADULACEÆ. Upper leaf-lobe much larger than lower; rhizoids borne in tufts on the lower leaf-lobes instead of on the stem; underleaves absent; perianth dorsiventrally compressed, smooth. Only genus *Radula*.

5.—SCAPANIACEÆ. Upper lobe of leaf smaller than lower; underleaves small or absent; perianth either cylindrical or dorsiventrally compressed, usually folded. Chief genera *Scapania*, *Diplophyllum*, *Gottschea*, *Balantiopsis*.

b. Leaves either entire, or with toothed or lobed margins, or deeply lobed, but with the lobes equal in size and form.

6.—PTILIDIACEÆ. Leaves generally with several long teeth or lobes; underleaves always present and

resembling the leaves in form and size; perianth with longitudinal folds and often concrescent with involucre. About a dozen genera, including *Ptilidium*, *Isotachis*, *Herberta*, *Polyotus*, *Trichocolea*, *Blepharostoma*.

7.—CEPHALOZIACEÆ (*Trigonantheæ*, Spruce). Leaves usually incubous; leaf-margin rarely entire, usually lobed or toothed; underleaves usually present, but smaller than the leaves and of different form; perianth usually hypogonanthous (*i.e.*, triangular in cross-section, with two dorsal angles and a ventral angle). About thirty genera, including *Cephalozia*, *Protocephalozia*, *Pteropsiella*, *Zoopsis*, *Lepidozia*, *Anomoclada*, *Mytilopsis*, *Micropterygium*, *Arachniopsis*, *Bazzania*, *Adelanthus*, *Marsupidium*, *Kantia*, etc.

8. LOPHOZIACEÆ (*Epigonantheæ*, Spruce. Leaves succubous or transversely inserted, entire or two-lobed; underleaves absent or small; perianth usually epigonanthous (*i.e.*, triangular in cross-section, with a dorsal angle and two ventral angles). About thirty genera, including *Lophozia*, *Haplozia*, *Nardia*, *Gymnomitrium*, *Marsupella*, *Plagiochila*, *Notoscyphus*, *Southbya*, *Arnellia*, *Tylimanthus*, *Lethocolea*, *Symphyomitra*, *Calypogeia*, *Saccogyna*, *Acrobolbus*, etc.

In the foregoing scheme, which is admittedly to a large extent artificial and provisional, I have suggested the elevation of the eight groups, which Schiffner (68) treats as sub-orders of Jungermanniaceæ, into independent orders. The only sharply marked and really natural families are the Lejeuneaceæ, Porellaceæ, Pleuroziaceæ, and Radulaceæ; the remaining four families are closely connected with each other and therefore difficult to characterise. This is especially the case with the Lophoziaceæ and the Cephaloziaceæ, which should, perhaps, be merged into one family. In these two families the perianth is quite as often as not a smooth or folded cylinder, neither distinctly "epigonanthous" nor "hypogonanthous"; the leaves are often quite as distinctly bilobed in Lophoziaceæ as in Cephaloziaceæ; the acrocarpous or pleurocarpous position of the archegonial group (and therefore of the sporogonium) varies in closely allied genera and even in species of the same genus (e.g., *Cephalozia*). That is, the two families cannot be kept apart by any of the characters generally used to distinguish them. The difficulty

of framing a natural classification is increased by the occurrence of many features which can only be regarded as examples of homoplasy. Among these parallel developments, may be mentioned the following, which are found in widely separated genera and families:—open water-pitchers (*Radula*, *Polyotus*, *Frullania*, etc.); closed pitchers with a trap-door or valve mechanism (*Pleurozia*, *Colurolejeunea*); paraphylls (*Gottschea*, *Trichocolea*, *Stephaniella*, *Marsupidium*); cœlocauly—the penetration of the stem by the sporogonium (*Gottschea*, *Trichocolea*, *Polyotus*, etc.); the formation of marsupia of various structural types (*Tylimanthus*, *Balantiopsis*, *Acrobolbus*, *Kantia*, etc.).

The Inter-Relationships of the Acrogynæ.

In discussing the inter-relationships of the Anacrogynous Jungermanniales, reasons were brought forward to support the view that the division of the Jungermanniales into Anacrogynæ and Acrogynæ is a purely artificial one. It was also suggested that the Anacrogynæ have arisen from a thalloid ancestor, and that the differentiation of stem and leaves has taken place in several diverging lines of affinity, starting from an undifferentiated thallus. On these views we must assume that the Acrogynæ have arisen from the Anacrogynæ, and of the two main series of Anacrogynæ it would appear that the *Pellia* series offers the natural starting-point for the Acrogynæ, since it is in the higher members of the *Pellia* line—in genera like *Fossombronia*—that we find the sharpest differentiation into stem and leaf.

The Lejeuneaceæ are so sharply distinguished from all the other Acrogynæ in the structure of the capsule, that some writers have inclined to the view that this group has arisen independently and that the Acrogynæ form a polyphyletic group, derived from the Anacrogynæ along two independent lines. Spruce was so deeply impressed by the marked characters of the Lejeuneaceæ that he divided the Jungermanniales into two groups—the "Jubuleæ" or Lejeuneaceæ forming one group, while his group "Jungermannieæ" included all the remaining forms, both Acrogynous and Anacrogynous. Schiffner (68) considered that the sporogonium of the Lejeuneaceæ shows such a degree of resemblance to that of the Aneuraceæ that he suggested the independent origin of the Lejeuneaceæ from a *Metzgeria*-like form, all the remaining Acrogynæ being derivable from a form like *Fossombronia*. This view is adopted by Lotsy (60),

who reproduces the general phylogenetic scheme suggested by Schiffner for the Acrogynæ. It is only fair to add that neither of these writers discusses the question in detail, and that both put their views forward in a tentative fashion. A careful comparison of the structure and development of the gametophyte and sporogonium in the Lejeuneaceæ and the Aneuraceæ shows that there are two points of apparent resemblance between these groups.

Taking first the sporogonial characters, which led Schiffner to suggest the possible origin of Lejeuneaceæ from Aneuraceæ, we find the resemblances are purely superficial. It is true that in both series elaters remain attached by their upper ends to the four valves of the dehisced capsule-wall, and that there is consequently a general similarity in the mechanism by which the spores are scattered. There are, however, fundamental differences in the structure and development of the capsule in the two families. In the Aneuraceæ, we find a solid mass of sterile tissue, forming an incomplete apical columella or elaterophore and splitting at dehiscence into four portions which remain fixed to the capsule-valves; some of the elaters are attached to this elaterophore, the rest being free and mingled with the spores. In Lejeuneaceæ, on the other hand, there is a regular alternation between (1) elaters fixed apically and extending the entire depth of the capsule-cavity, and (2) longitudinal rows of spores; there is no elaterophore, and all the elaters are fixed. The occurence of elaters fixed by their upper ends to the inside of the capsule-wall in various genera of Acrogynæ widely removed from the Lejeuneaceæ in the current system of classification forms an additional argument, if any be necessary, against the existence of any close connexion between the Aneuraceæ and the Lejeuneaceæ as regards the structure of the sporogonium. The Lejeuneaceous capsule is, in fact, much more readily derived from that of, say, *Cephalozia* or *Lepidozia*, than from that of *Aneura* or *Metzgeria*. In *Cephalozia*, *Lepidozia*, and several other genera, most, if not all, of the elaters are fixed by one end to the capsule-wall and radiate towards the centre and the base of the capsule-cavity (Fig. 50, IV.), and from this type the arrangement characteristic of the Lejeuneaceæ can easily be derived. The resemblances between the Aneuraceous and Lejeuneaceous types of capsule-structure appear, in short, to be entirely illusory.

Much more striking is the resemblance between the Aneuraceæ and Lejeuneaceæ in the early stages of development of the gametophyte. Except for the absence of a midrib, the thalloid vegetative

plant-body of *Metzgeriopsis*, which may be regarded as a persistent protonema, agrees exactly with the thallus of a *Metzgeria*. The early stages in germination of the spore are precisely alike in *Metzgeria* and the Lejeuneas; in both cases, after one or two transverse divisions have taken place in the short germ-tube, the distal cell gives rise to a two-sided apical cell and a ribbon-like protonema is formed. In *Metzgeria* and in *Metzgeriopsis* the protonema continues to grow as a flat thallus; in *Metzgeria* a midrib is formed and the protonema develops directly into the adult thallus, while in *Metzgeriopsis* the persistent protonema or thallus gives rise eventually to the leafy sexual shoots. Moreover, *Metzgeria* and the Lejeuneæ agree in producing discoid gemmæ, but in this respect the two genera simply illustrate what appears to be a general rule in the Hepaticæ, namely, that the protonema and the gemmæ of any given species usually show a close resemblance in form.

As an indication that too much stress should not be laid upon the mode of germination and the form of the protonema in the different groups of Hepaticæ, it may be pointed out that there are great variations in this respect amongst allied forms. The germination of a considerable number of Hepaticæ has been described by Grönland (37), Leitgeb (56), Campbell (3), Frau Lampa (51). Douin (9), Goebel (32), and others. In Hepaticæ, as in Mosses, the development of the gametophyte is "heteroblastic," since there is first formed a protonema or "pro-embryo" of simple form, and from this the adult plant arises, usually from a terminal cell which becomes the apical cell of the plant-body. As a rule, the spore contents grow out to form a positively heliotropic and usually unbranched filament or germ-tube in the first instance, and the apical cell of the adult plant may either arise from the terminal cell of this filament (most Acrogynæ), or the formation of a germ-tube may be more or less completely suppressed so that the protonema forms a cell-surface or disc; the young plant arising from one of the marginal cells. A germ-disc is formed directly from the spore in *Radula*, for instance ; in *Frullania* and *Porella*, divisions occur in all directions of space, producing a solid ovoid protonema instead of a discoid cell-surface. In various other genera of Acrogynæ, we find transitions from the germ-tube to the germ-disc types of protonema; sometimes both types are found in the same species.

In the other groups of Hepaticæ, we find similar diversity in the form of protonema. Among the Anacrogynæ, *Aneura*

resembles *Metzgeria*, except that sometimes the protonema is at first filamentous and may even undergo branching before giving rise to a cell-surface and developing into the adult thallus. In *Pellia*, an ovoid cell-mass is formed by the germination of the spore while still within the capsule, a hyaline cell at one end producing the first rhizoid when the spore is shed, while the growing-point arises from the other end; or both ends may produce a rhizoid, while the growing point arises in the middle of the protonema. In *Blasia*, the cell-mass from which the thallus arises may either be produced from the terminal cell of a germ-tube, or the latter may be suppressed so that the cell-mass arises directly from the spore. The germination of *Fossombronia*, according to Frau Lampa, is somewhat remarkable—the end-cell of the germ-tube gives rise to a three-sided apical cell, producing three rows of leaves, though the apical cell of the adult plant is two-sided and the leaves are in two rows.

In the Marchantiales, *Fegatella* resembles *Pellia* in that the spore germinates before leaving the capsule, forming an ovoid cell-mass, and Frau Lampa states that when the multicellular spore, or protonema, is set free it grows at first by a three-sided apical cell and is cylindrical, but later acquires dorsiventrality and gives rise to the adult thallus. The same writer also describes the cell-mass formed in various genera of Marchantiales by division of the end-cell of the germ-tube, as growing at first by a three-sided apical cell and producing three rows of leaves, which are especially definite in *Preissia*.

As already stated, there are many cases in which the form of the Hepatic protonema varies between the two main types—the filamentous and the discoid—in the same species. Moreover, it has been shown, by Schostakowitsch (74) and others that the structure and duration of the protonema can be altered at will by controlling the external conditions under which the spore germinates, and that light-intensity is the most important of these conditions. For instance, the normally short-lived filamentous protonema of *Cephalozia*, *Chiloscyphus*, etc., can be cultivated for many months in feeble light without producing leafy shoots; the protonema branches freely, like the protonema of a Moss or the filamentous vegetative body of *Protocephalozia*. In the Marchantiales feeble light inhibits the formation of the germ-disc and therefore of the adult thallus; if a germ-disc has been formed, reduction in light-intensity causes it to give out filaments, on

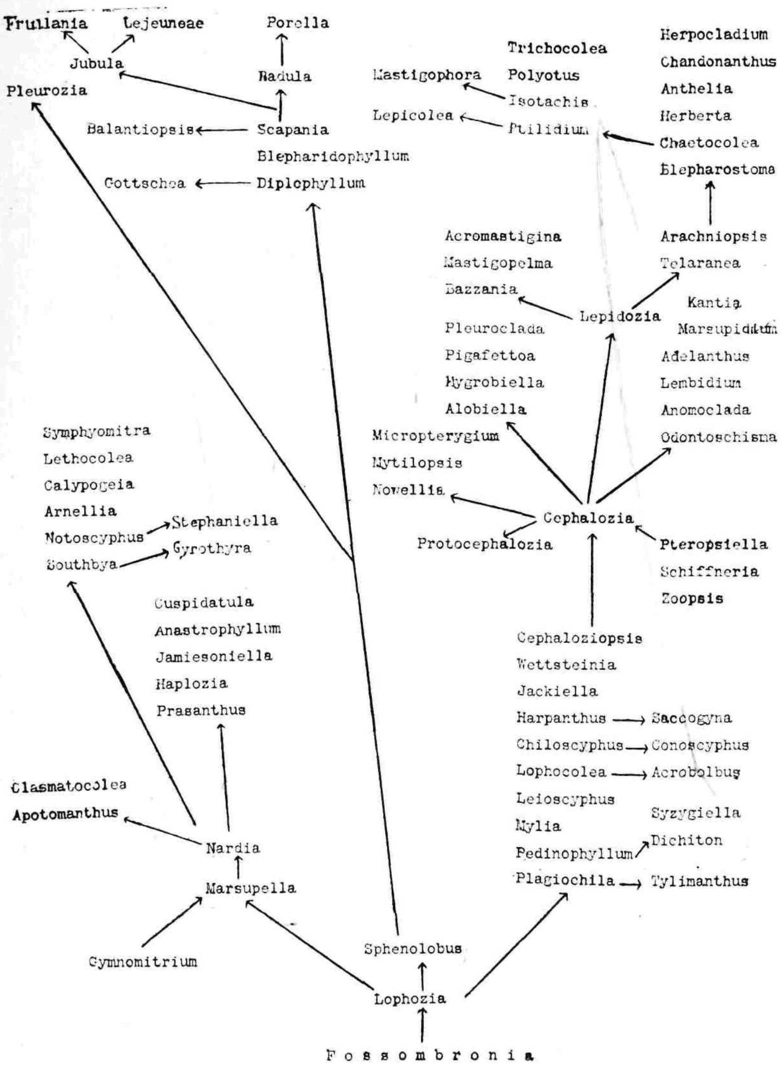
which further germ-discs are produced on exposure to stronger light, and so on. Again, if the protonema of a leafy Hepatic has already given rise to the young leafy shoot, exposure to weak light inhibits the development of the adult type of leaf, so that we get a slender plant with rudimentary leaves; this state of things occurs normally in *Zoopsis*, a genus allied to *Cephalozia*. Without going further into details, it may be said that all the phenomena of arrested development which can be induced artificially, or which occur occasionally, in almost any Liverwort, also occur regularly in nature in certain species.

However, we shall discuss later certain questions bearing upon the phylogeny of the Bryophyta in general which arise from the phenomena of juvenile stages and of naturally occurring as well as artificially induced variations in the form of the gametopyte. There is much need for further observations on the germination of Hepaticæ, and for work in experimental morphology in this group. From what has been set forth here, it would appear that the resemblances between the Aneuraceæ and Lejeuneaceæ in the form of the protonema cannot be regarded as indicating any real link between the two groups. We are therefore driven to the conclusion that the Acrogynæ form a monophyletic series.

A careful survey of the Acrogynæ suggests that the following may be regarded as relatively primitive gametophytic characters:—leaves symmetrically bilobed more or less deeply, and either flat or only slightly folded; underleaves present; archegonia borne on the main axis; perianth free from the involucre and either cylindrical or corresponding to three flat leaves carried up by common basal growth; protonema filamentous. On the other hand, we may regard as advanced or specialised characters the complete absence of lobing from the leaf, or on the contrary its division into several deep lobes, or its division into two lobes of very unequal size; the absence of underleaves; the restriction of the archegonia to special short branches; the fusion of the perianth with the involucre, lateral or dorsiventral flattening of the perianth, and the development of wings on its exterior; discoid protonema; and, finally, various elaborations such as the formation of pitchers, paraphylls, marsupia, etc. Many of these advanced and specialised characters have arisen independently in different lines of affinity, and are to be classed as parallel developments.

Assuming that the Acrogynæ have arisen from a *Fossombronia*-like type, it is probably among the Lophoziaceæ or the

Cephaloziaceæ that we should look for a form presenting the greatest resemblance to *Fossombronia*, and, at the same time, the most primitive Acrogynous characters. On the whole, perhaps the genus *Lophozia* may be selected as a good starting-point for the evolution of the Acrogynæ. In *Lophozia*, the branching is practically dichotomous, the leaf-insertion varies from transverse through succubous to nearly longitudinal, the leaves are more or less deeply and symmetrically bilobed, the underleaves are small



Phylogenetic scheme of the *Acrogynæ*.

(in some species absent), the archegonia are developed on the main shoots, the perianth is cylindrical and free from the involucre. From *Lophozia* we can trace three main lines. (1). One line leads directly through *Sphenolobus* to the Scapaniaceous genera *Diplophyllum* and *Scapania*, in which the leaves are deeply lobed, the upper lobe being smaller than the lower and the insertion succubous. (2). A second line leads through a long series of genera with relatively simple characters (*Plagiochila*, *Lophocolea*, etc.) to genera to in which the archegonia are shifted on to short lateral branches (*Chiloscyphus*, *Harpanthus*, etc.), and which in this and other respects form a transition to the Cephaloziaceæ through intermediate types like *Cephaloziopsis*, *Cephaloziella*,, and *Cephalozia* itself. Several marsupial genera arise from this line, e.g., *Tylimanthus* and *Acrobolbus*, which are allied to *Plagiochila*, and *Saccogyna* which resembles *Harpanthus* in vegetative characters. (3). The third line is marked by the reduction in size of the perianth, fusion of perianth with involucre, and the development of marsupia; this line begins with *Marsupella*, and leads through *Nardia* to the marsupial genera *Southbya*, *Calypogeia*, *Lethocolea*, etc.

In the *Cephalozia* series, three lines start from *Cephalozia* itself. (1). One of these is marked by more or less far-reaching reduction of the leaves, leading to forms like *Zoopsis* and *Pteropsiella*, the latter becoming thalloid owing to the "fusion" of the leaves with the stem, while *Protocephalozia* has a persistent filamentous protonema, leaves being produced only on the sexual shoots.. (2). A second line, in which the leaves are only slightly lobed or quite entire and the archegonia are restricted to very short ventral branches, leads through *Odontoschisma* and *Adelanthus* to the marsupial genera *Marsupidium* and *Kantia*—the only marsupial forms in the Cephaloziaceæ.. (3). The third line, characterised by the division of the leaf into increasingly numerous and deep lobes, leads through *Bazzania* and *Lepidozia* to *Arachniopsis* and *Telaranea*, which closely resemble the Ptilidiaceous genus *Blepharostoma* and form a transition to this family.

The Ptilidiaceæ, though a small family, shows several diverging lines of development, all of which appear to end blindly. In the majority of the genera, the archegonial group is terminal on the main axis; in the others (*Ptilidium*, *Lepicolea*, *Mastigophora*, *Isotachis*) it is on a short branch, but this is lateral—not ventral, as in the Cephaloziaceæ. A very marked character of the family

is the agreement in form and size between the leaves and the under-leaves—a character found only in *Lepidozia* among the Cephaloziaceæ. With the latter family the Ptilidiaceæ agree in the form of the perianth, which is either cylindrical or triangular with one angle ventral; this sharply separates the Ptilidiaceæ from the Lophoziaceæ, in which the perianth when triangular has one angle dorsal. In this small but interesting and diversified family we find a number of features which recur in various other families of Acrogynæ, and which are examples of parallelism, *e.g.*, the development of paraphylls in *Chandonanthus* and *Trichocolea*, the *Frullania*-like pitchers of *Polyotus*, the "midrib" of elongated cells in the leaves of *Herberta*.

The Scapaniaceæ, which may be derived from a *Lophozia*-like type, present various features which recur in other families, *e.g.*, the winged leaf *Gottschea* (cf. *Micropterygium*) and the marsupium of *Balantiopsis*. The most marked vegetative peculiarity of this family is the small size of the dorsal as compared with the ventral lobe of the leaf. However, in some species of *Scapania* the two lobes are equal in size, or nearly so.

The remaining four families agree with each other and differ from the rest of the Acrogynæ in the deep division of the leaf into a large dorsal and a small ventral lobe, the two lobes being sharply folded against each other, and in the discoid form of the protonema and of the gemmæ. In none of these four families is a marsupium formed, and the perianth is never concrescent with the involucre. Each family presents strongly marked characters of its own, but they are probably connected with the other Acrogynæ through *Radula* and *Scapania*. In some species of both these genera, the two lobes of the leaf are equal in size, and the two genera further agree in having a dorsiventrally flattened perianth. *Porella* agrees with *Radula* in general habit, but it has under-leaves, the archegonia are on special short branches, and the upper end of the seta is expanded to form an apophysis. *Jubula* is probably related to *Porella*, and from *Jubula* we can derive on one hand the genus *Frullania* and on the other the Lejeuneæ. *Pleurozia* is a somewhat isolated genus, and it is probably more nearly related to the *Lophozia* series than to *Porella* and *Radula*, with which it is associated in the scheme of classification.

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V. ANTHOCEROTALES.

IN Schiffner's account of this family in Engler and Prantl (32), three genera are distinguished: *Anthoceros* (cosmopolitan, with 79 species), *Dendroceros* (tropical, with 15 species), and *Notothylas* (temperate and tropical, with 9 species.) At the present time, the number of species described stands at about 120, all growing on damp soil with the exception of a few *Anthoceros* species, which occur on decaying wood, and of all the *Dendroceros* species, which are epiphytic on the stems and even on the living leaves of tropical trees.

In most species of *Anthoceros* the thallus is, as in the widely distributed *A. lævis*, several cells thick at the middle and thins out to a single layer at the margin, where there are numerous growing points each occupying a notch. The apical growth can usually be referred to a single initial cell, from which segments are cut off above, below, and on either side. The further divisions of the segments are very regular; each upper and lower segment divides first into an inner and an outer cell, the inner cells derived from both segments giving rise to the central tissue of the thallus, while the sexual organs on the upper side and the rhizoids and *Nostoc*-cavities on the lower are derived from the outer cells of the segments. The thallus branches repeatedly and rapidly, and often in such a regularly dichotomous manner as to form a more or less regular disc, or rosette, of circular outline. When branching is about to occur, the apical cell divides so as to form a row of cells lying side by side, and the middle cells then grow out and form a projection ("middle lobe") separating the two new growing-points.

These middle lobes usually remain small, but in some species they grow into conspicuous appendages, often toothed, which serve to retain water by capillarity and also to increase the assimilating surface of the plant. The same purpose is served by the leaf-like outgrowths on the upper side of the thallus in some species; in *A. fusiformis* these are lamellæ of varying sizes and shapes, while in *A. arachnoides* the whole plant is covered with hair-like or plate-like outgrowths forming an irregular network of shallow water-holding chambers. In *A. giganteus* the thallus is sharply divided into a massive midrib and one-layered wings, the lobes of the latter being folded over towards the underside and forming hood-like water-cavities.

Many species of *Anthoceros*, especially those which grow in dry situations, have perennating tubers in which food is stored and which persist after the rest of the plant has died down. In most cases these tubers arise on the edge of the thallus, probably always from a growing-point, and either remain as swollen bodies slightly buried in the soil, or they may become stalked and pushed well below the surface. Examples of tuber-bearing species have been figured by Howe (14) and by Goebel (9); as was shown by Ashworth (1), the tuber has a firm envelope of corky cells, while the inner cells contain proteid-grains and oil-drops.

The tissues of the thallus are usually almost uniform, though the central cells are often, especially in the older parts of the thallus, greatly elongated and have their walls reticulately thickened. Though not forming a very definite strand, these cells may perhaps be compared with the pitted cells forming the conducting tissue in such Liverworts as *Pallavicinia*, but it must be remembered that similarly thickened cells often occur in the Marchantiales. In several species of *Anthoceros* there occur cavities of irregular shape and size, which are formed by splitting apart of the cells and contain abundant mucilage. In *A. dichotomus*, of which the writer has examined abundant fresh material, these mucilage sacs are sometimes inhabited by *Nostoc*, the chains of this alga having apparently entered the otherwise quite closed sacs by way of the intercellular spaces; in some cases the *Nostoc* chains were seen to be connected with the normal *Nostoc*-cavities which at first open by a stoma-like slit on the underside of the thallus. The *Anthoceros* thallus does not bear the special gum-forming hairs which are so common in Liverworts, but the special mucilage-slits, to be described presently, keep the growing-point bathed in

gummy liquid. Indeed all the tissues contain abundant mucilage, which escapes when the thallus is cut into.

The thallus shows two vegetative features of special interest, the peculiar chloroplasts and the *Nostoc*-cavities. In nearly every cell there is, in most species of *Anthoceros*, a single large chloroplast, varying in form. but usually oval and flattened, with a conspicuous central pyrenoid, around which starch-grains are clustered as in various Green Algæ with similar chloroplasts. The nucleus lies in close apposition to the chloroplast, usually near the pyrenoid, and sometimes the chloroplast becomes folded so as to enclose the nucleus more or less completely. The curious *Nostoc*-cavities almost always found in the lower tissue of the thallus were described by Hofmeister (13), who mistook them for gemmæ; what he figures as cell-walls dividing up the cavity are in reality the hairs which grow in from the cells bounding the chamber after the *Nostoc* has entered by means of a slit between two of the lower superficial cells of the thallus. The real nature of these cavities was discovered by Janczewski (17) and Szymanski (34), while Leitgeb (22) carefully followed the development of the cavities and their infection by the hormogonia of *Nostoc* and showed how the *Nostoc*-chains grow vigorously in the enlarging cavity, the cells lining the latter growing into hairs which mingle with the alga. These cavities are primarily gum secreting organs, and Peirce (30) has recently shown that *Anthoceros* plants raised from spores in sterilised soil grow quite normally, and probably even better, in the absence of *Nostoc*.

Apart from Hofmeister's "gemmæ," which turned out to be the *Nostoc*-cavities just mentioned, there are some observations on record which seem to indicate that *Anthoceros* has special organs for asexual propogation. Hofmeister's account of small gemmæ which arise by rejuvenescence of the mother-cell and escape through a pore in the wall does not appear to have been confirmed, though gemmæ, or more correctly *gonidia*, of this nature occur in *Aneura* and *Metzgeria*. Ruge (31) has described and figured the development in *Anthoceros glandulosus* of stalked brood bodies which have a mucilage cavity and pore already formed before being detached from the parent plant.

The sexual organs of the Anthocerotales differ very markedly in certain respects from those of other Bryophytes, though their peculiarities have been somewhat exaggerated by some writers. In the case of the antheridia, either one, or (in *Notothylas* and

most species of *Anthoceros*) a group, of these organs occurs in a closed cavity in the upper tissue of the thallus, roofed over by a double layer of cells, this roofing tissue being later ruptured so that the antheridia are left in a cup-like depression. According to most recent writers, the antheridium, or group of antheridia, arises from a single superficial cell which divides first by a transverse wall into an inner and outer cell, the latter dividing again by a tangential wall to form the beginning of the roof, while the inner cell divides longitudinally into four parallel cells, which either remain coherent and develop into a single antheridium, or else separate and form four antheridia. Apart from their endogenous origin, the antheridia agree in structure with those of the Sphærocarpales. The number of antheridia in each cavity varies a good deal in different species of *Anthoceros*, and in different individuals; there may be as many as nine or ten. As first described by Leitgeb (23), exogenous antheridia sometimes occur in *Anthoceros*, evidently through an inversion of the normal course of development—*i.e.*, the upper half of the primary cell gives rise to the body of the antheridium and the lower to the stalk. Frau Lampa (18) has described, as exogenous antheridia what appear to be in reality the early stages of the tubers found in *Anthoceros dichotomus*. Though the occurrence of exogenous antheridia is apparently a rare abnormality in *Anthoceros*, it probably represents a reversion to a primitive condition, and it would be interesting to ascertain whether it occurs in other species of *Anthoceros* besides *A. lævis*, and in the remaining genera of the group.

The archegonia of the Anthocerotales are not only sunk in, but are from the beginning histologically continuous with, the tissues of the gametophyte. However, the cell-divisions that occur in the developing archegonium are exactly the same as in the other Liverworts; the mother-cell does not project from the surface, but it undergoes the usual three primary intersecting divisions, cutting off the peripheral cells (which in other Bryophytes form the venter and neck) from the central cell which divides to form the usual axial series of the Liverwort archegonium (cover-cell, neck-canal-cells, ventral-canal-cell, oosphere). The cover-cell-group often projects slightly, and it would be of great interest if cases were discovered in which more or less of the neck is free. As it is, the difference between the Anthocerotean archegonium and that of other Bryophytes is merely one of degree, and the gap is to some extent bridged over by *Aneura*, where the venter is

embedded in and continuous with the thallus tissue, instead of being entirely free on the surface.

The oospore divides by longitudinal and transverse walls so as to form three tiers of four cells each, and in all probability these tiers give rise to the three regions of the mature sporophyte—the more or less bulbous foot, the meristem, and the capsule. The cells of the upper tier are next divided by walls which cut off four central cells from a layer of outer cells; but now the course of development diverges from that typical of other Liverworts. In the latter, the central tissue (endothecium) becomes the sporogenous tissue, but here it remains sterile and forms an actual rod or columella, while the archesporium is cut out of the peripheral layer and, moreover, is hemispherical, extending over the apex of the columella (this is the case with the *fertile* portion of the archesporium in *Pellia*). The original four rows of cells forming the columella increase to sixteen rows, the archesporium becomes two-layered, and the capsule-wall becomes about four cells deep, the outermost layer forming a sharply marked epidermis with cuticle and stomata. The cell-divisions in the meristem zone below the capsule correspond with those in the capsule region of the embryo, and owing to the active growth of this zone the capsule continues to elongate for a considerable time, additions being made to columella, archesporium, and wall. The archesporial cells become differentiated into large globular spore-mother-cells and variously shaped sterile cells which remain irregularly united to form a network. The cells forming the sporogonial wall are separated by air-spaces which communicate with the stomata in the epidermis, and each cell contains *two* chloroplasts. The stomata are quite like those of the Vascular Plants; each is formed by splitting of a cell which has remained oval while the surrounding epidermal cells have become elongated. As the spores ripen, the capsule-wall splits, from the apex downwards, into two valves, between which the thread-like columella projects. The columella has a mechanical function in strengthening the long sporogonium and holding together the network of sterile cells with the spores in its irregular meshes, but its primary function is doubtless that of transporting water and salts, absorbed from the thallus by the foot, to the green assimilating tissue of the capsule-wall, by way of the sterile cells, as well as to the developing sporogenous tissue. The sterile cells when young contain abundant starch and proteids. The developing spores are therefore very efficiently supplied with food by

means of the columella, the sterile cells, and the green tissue, and their rapid development is obviously due, as pointed out by Goebel (10) to these favourable arrangements for their nutrition. The sterile cells of *A. lævis* are thickened along two opposite sides of the wall, which in some cases even shows distinct spiral thickening bands. The latter are well developed in *Dendroceros* and in certain species formerly included in *Anthoceros*, but now transferred to Campbell's new genus, *Megaceros*. There can be little doubt, from actual observation, that even in *A. lævis* the sterile cells perform, as their final function, some service in aiding spore-dispersal by means of hygroscopic movements. For some time the surrounding tissue of the thallus, into which the bulbous foot penetrates deeply and sends haustorial outgrowths of its outer cells, keeps pace with the growth of the sporogonium and grows up as a sheath, which is eventually broken through at the tip. The capsule reaches a length of as much as four inches in some species, giving fruiting patches of the plant the appearance of fine grass, and continues to grow for months. In germination, the spore-contents usually give rise to a longer or shorter germ-tube, at the end of which a cell-mass is formed, but sometimes the tube is suppressed; in any case the cell-mass soon shows an apical cell, rhizoids, mucilage slits, and apical branching.

In *Dendroceros*, the plant-body is distinguished into a thick and usually broad midrib with one-layered lateral wings, which are folded and often regularly lobed, showing an approach to the *Fossombronia* type with distinct leaves. Some species are definitely foliose, and in *D. foliatus*, discovered by Spruce (33), large hood-like structures are developed from the "middle lobes" formed in branching, in addition to smaller hidden appendages which represent the ordinary lobes or leaves. As in *Anthoceros* there are *Nostoc*-cavities, and in some species large intercellular cavities in the midrib, giving the latter an areolated appearance like that of a Marchantiaceous thallus. The development of this genus has been chiefly worked out by Leitgeb and by Campbell (3). The apical cell is semi-circular, segments being cut from it in a single series. The antheridia are solitary, large, and long-stalked the stalk is coiled up within the cavity, the roof of the latter projecting strongly above the surface of the thallus. The sporogonium on the whole resembles that of *Anthoceros*, except that the archesporium extends downwards nearer to the foot and often remains in parts only one cell thick, the sterile cells becoming

joined end to end and forming definite elaters with a well-marked spiral band ; there are no stomata on the capsule. In some species the spores begin to germinate before being set free, forming multicellular bodies, as in *Pellia* and *Fegatella*.

Notothylas shows a close general resemblance to *Anthoceros* in its gametophyte and sexual organs, but the sporogonium presents some interesting points of difference and has given rise to much discussion and conflicting opinion. Lang's recent work on this genus (20) has added considerably to our knowledge of the sporogonium and its development. The earlier observers Milde (26, 27, 28) and Gottsche (12) held that the columella of *Notothylas* might either be present or absent in different plants of the same species, and that it might be either intact and well-developed in mature or nearly mature capsules, or might be broken into fragments, or represented by a short projection at the base of the capsule. Leitgeb confirmed these observations, but showed that when the columella was absent this was not due to breaking up into its constituent elater-like cells, as Gottsche had suggested. Leitgeb further concluded that while the first divisions of the embryo were like those of *Anthoceros*, the central (endothecial) cells cut off by the first periclinal walls gave rise to the archesporium and that the columella was subsequently differentiated within this central tissue or endothecium. Leitgeb found the columella well developed in some specimens of *N. Breutelii*, while in others there was hardly a trace of it even at the base of the capsule, and on the view that the whole sporogenous mass is derived from the endothecium and the columella arises by later differentiation within it, he suggested that this genus forms a link between the other Anthocerotales on one hand and the Jungermanniales on the other, comparing the columella of *Notothylas* to the axile bundle of sterile elater-like cells which springs from the base of the capsule of *Pellia*.

According to Mottier (29) and Campbell (2) the development of the sporogonium in *Notothylas orbicularis* is much the same as in the other Anthocerotales, except that the archesporium becomes very massive in its upper part where it extends over the apex of the columella. These writers confirm Leitgeb's account, however, as to the regular alternation of alternate zones of sterile and fertile tissue in the archesporium, and the occurrence of curved thickenings on the sterile cells and also on the cells composing the columella. Lang's account is much more complete and conclusive, and he sums up the chief features of the sporogonium in the species he investi-

gated (*N. Breutelii*) by saying that "the embryogeny conforms to the usual type for the Anthocerotaceæ, but that the endothecium, instead of being devoted to the formation of a sterile columella, forms sporogenous tissue for the greater part of the intercalary growth of the sporogonium. In a considerable proportion of cases, however, it produces sterile tissue towards the close of development." His observations show that the endothecium must be regarded as potentially sporogenous, a fact which, according to this writer, "increases the justification for considering the central group of cells, which in all other Anthocerotaceæ is wholly devoted to the formation of a sterile columella, as the original sporogenous tissue and the amphithecial archesporium is of secondary origin. The duty of producing spores would seem to have been transferred from the central to a more superficial set of cells." Lang inclines to the view that the species of *Notothylas* are reduced forms, since "the appearance of the archesporial layer derived from the amphithecium, even when the central cells are fertile, suggests an origin from forms with a sterile columella."

Among some specimens from the herbarium of Mr. W. H. Pearson, the writer found a species of *Anthoceros* (*A. Hallii*, Aust.) which differs considerably from the rest of this genus and approaches closely to *Notothylas*. The sporogonium of *Notothylas* is very small and when ripe projects but slightly beyond the "calyptra" or sheath; its epidermis has no stomata; there is practically no assimilating tissue; and the inner layers of the capsule-wall soon become disorganised (probably serving to nourish the developing spores). In *Anthoceros Hallii* the capsule (4 to 7 mm. long) projects beyond the sheath for less than one-third of its length. The projecting apical portion bears a small number of remarkably large guard-cells; each cell of the capsule-wall contains two large chloroplasts; the columella does not extend into the projecting tip of the sporogonium; and the sterile cells have the stumpy flattened form characteristic of *Notothylas*, and bear irregular fibrous thickenings. *Anthoceros Hallii* appears to form an almost perfect connecting-link, in such characters as can be made out from herbarium material, between the small-capsuled species of *Anthoceros* on one hand and the forms included under the genus name *Notothylas* on the other.

It has long been known that certain species hitherto included in the genus *Anthoceros* resemble *Dendroceros* in having the sterile cells developed as elaters with spiral bands, and in the absence of

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stomata from the capsule-wall. Campbell (4, 5, 6, 7) has recently investigated a number of these species and has proposed the formation of a new genus, *Megaceros*, for their reception, the name being suggested by the large size of the sporogonium in most of these forms. This genus is further distinguished from *Anthoceros* by having green spores, a solitary antheridium, and as a rule several chloroplasts in the thallus-cells instead of a single large chloroplast. This new genus presents interesting points of contact with the other three genera of Anthocerotales. It resembles *Anthoceros* in the form of the thallus and its apical growth, and in the form and size of the sporogonium; *Notothylas* in the large amount of sporogenous tissue developed in the apical region of the sporogonium, above the columella; and *Dendroceros* in the characters already mentioned above, also in the green spores and the early development of the embryo.

The facts at present known concerning the morphology of the Anthocerotales appear to the writer to suggest that (i.) the forms constituting Campbell's genus *Megaceros* are at least as sharply separated from the other species of the old genus *Anthoceros* as are those comprised in the genus *Notothylas*; (ii.) the species of *Dendroceros* form a still more natural group; (iii.) it is an open question whether *Notothylas* is a reduced form. The organisation of the *Notothylas* sporogonium need not necessarily be interpreted as due to reduction from the *Anthoceros* type; the reverse interpretation does not appear to be excluded by the fact that both the endothecial and the inner amphithecial tissues produce spores. Apart from the close agreement of its gametophyte with that of *Anthoceros*, we find in the *Notothylas* sporophyte a series of forms showing varying and unfixed sterilisation of the central tissue, with progressive shifting of spore-production to the inner layer of the wall-tissue. Assuming the absence of reduction in the *Notothylas* types, we might regard *Anthoceros Hallii* as forming a link between the more primitive forms of *Notothylas* and the species of *Anthoceros* with stomata and well-developed assimilating tissue, while *Megaceros* and *Dendroceros* have arisen independently from the primitive forms of *Notothylas*, in which the sterile cells of the archesporium are short and isolated, the assimilating tissue of the sporogonium is feebly developed, and stomata are not formed. If we regard the typical *Anthoceros* capsule, with its stomata and its efficient assimilating arrangements, as being primitive, we must

assume that all the other Anthocerotales have been derived from this type by more or less extensive reduction.

Various writers have emphasized the characters which mark off the Anthocerotales from the remaining Hepaticæ, and in 1897 Gayet (8) proposed to raise the Anthocerotales to the rank of a class co-ordinate with the Hepaticæ, restricting the latter term to the Marchantiales and Jungermanniales. The class was named Anthocerotes by Howe (14), who defined it in the formal systematic way, enumerating the peculiarities of the class as follows: "(i.) a single large chloroplast to each cell, instead of several smaller chloroplasts as in the assimilative tissues of the Hepaticæ proper; (ii.) the antheridia arise within the thallus—are endogenous in origin—and the walls of the immersed archegonia are confluent with the adjacent tissues; (iii.) the presence of meristematic tissue in the capsule near its base, by the activity of which the capsule has a long continued growth, ripening spores towards its apex while forming new spore-mother-cells below; (iv.) the presence, in probably all cases, of a columella around which the archesporium is formed; (v.) the presence, in many cases, of stomata on the capsule, with accompanying assimilative tissue. These five characters are peculiar to the Anthocerotes as distinguished from the Hepaticæ proper, and they are characters of much significance. For analogies we must look chiefly in two directions—toward the Pteridophyta and toward the Musci."

In the writer's opinion, the significance of these characters of the Anthocerotales has been much exaggerated, and upon them has been based a certain amount of very doubtful speculation regarding the relationships of the Archegoniatæ and the origin of the Pteridophyta. From the summary presented here, it will be seen that very little importance can be attached to the first and second of the characters mentioned above. The number of chloroplasts per cell varies considerably. The "endogenous" origin of the antheridia is obviously a secondary character, derived from the normal exogenous type of antheridium development; the antheridia themselves agree closely with those of other Hepaticæ, especially Sphærocarpales, and though the development of the antheridial cavity is peculiar, it is easier to relate it to what is found in other Hepaticæ than to establish analogies with the Pteridophyta. In the immersion of the archegonium in the thallus, the Anthocerotales do not in reality differ widely from other Hepaticæ; the archegonium is partly embedded in *Aneura*, though in this case the neck is free. The

meristematic tissue above the haustorium of the sporogonium in Anthocerotales evidently results from the persistence of a stage which is quickly passed through in the development of the sporogonium in other Hepaticæ. In *Pellia*, for instance, the cells of the seta are arranged in regular longitudinal rows, owing to repeated transverse divisions in the cells between haustorium and capsule, and we may imagine the sporogonium of Anthocerotales to have arisen through the persistence of the meristematic activity of this zone of tissue, the differentiation of the capsule being deferred and becoming basipetal, instead of taking place early and being simultaneous. The columella of the Anthocerotean capsule, again, may be compared with the incomplete sterilisation of central tissue which results in the formation of the elaterophore of such forms as *Pellia*, *Aneura*, and *Gottschea splachnophylla.* It is doubtful whether much stress should be laid on the presence of stomata in the epidermis of the *Anthoceros* capsule; this feature is doubtless to be correlated with the development of a many-layered capsule-wall consisting of assimilative parenchyma. In various Jungermanniales, the capsule-wall is many-layered, and when young contains chloroplasts—a condition which persists in the Anthocerotales, but is also found in the ripe capsules of forms like *Riella*, where the cells of the capsule-wall do not become thickened with fibres in connection with a special dehiscence mechanism.

It seems probable that the Anthocerotales have arisen from forms like the Sphærocarpales, along a well-marked line of development which has led no further, and which is marked mainly by the "endogenous" origin of the antheridia and by the retention of a basal meristematic zone in the sporogonium. The antheridia were doubtless originally exogenous, and instead of becoming surrounded by an envelope (as in Sphærocarpales) or sunk in an open pit (as in Marchantiales and various Anacrogynous Jungermanniales), they have become sunk in a closed cavity formed by splitting of the walls between the antheridium-forming hypodermal cell and the surrounding thallus cells. The occurrence of a group of antheridia formed by longitudinal splitting of the young antheridium, is clearly a secondary character, just as is the process of budding which leads to the formation of more than four antheridia in a cavity in some species of *Anthoceros.* All the distinguishing characters of the Anthocerotean sporogonium are more or less definitely correlated with the persistence of the basal meristematic tissue, and are connected with the nutrition of the spores. The basal meristem

produces sporogenous tissue which becomes carried up and thus separated more and more widely from the tissues of the gametophyte. In this way there is set up a demand for more elaborate and more permanent nutritive arrangements than are required in the other Hepaticæ, in which the developing sporogonium is until maturity more or less completely surrounded by the tissues of the gametophyte.

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VI. SPHAGNALES.

THE general vegetative characters of *Sphagnum*, the sole genus in this group, are, perhaps, too well known to require detailed treatment here. The stems, individually weak, gain support by their dense aggregation when growing, as is usual, in cushions above the surface of the water, the closely crowded branches at the top being either pale-green or showing various shades of red, yellow, or brown, while lower down the plants are brownish or dirty-white. The length to which the stems may grow is practically indefinite, and when the plants occur loosely in pools they may be several feet long. The branches arising from the main stem are of three kinds, without counting those which bear the antheridia and archegonia. At the apex of the plant the branches are short and so crowded as to form a compact head or "coma" (Fig. 55), but lower down they are spaced out in tufts on the stem, usually at every fourth stem-leaf, and each tuft may consist of from three to about eight branches. In one species (*S. monocladum*) the branches are single, and in a few cases there are more than eight branches in a tuft. In the submerged species and varieties, growing in bog pools, all the branches are similar in form and structure and spread out from the stem, but in other cases some of the branches of each tuft stand out (divergent branches) while the rest are longer and more slender and droop, lying close to the stem and covering it as with a loose mantle (Fig. 56). At intervals one of the branches in a tuft, instead of forming a divergent or pendent short branch, grows upwards, repeats

the structure of the main stem, and reaches the same height as the latter.

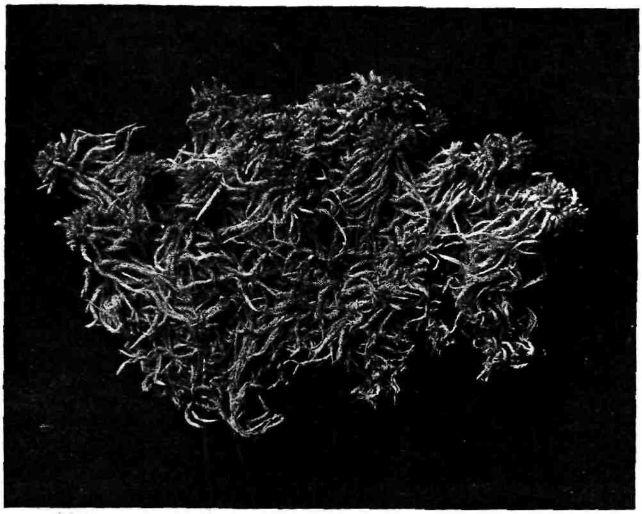

Fig. 55. Portion of a tuft of *Sphagnum acutifolium*, nat. size.

The stem, and each of its branches, grows by means of a three-sided apical cell (Fig. 57A), the segments becoming displaced very early from the three-rowed arrangement so that the leaves come to form usually five rows (Fig. 58). Each leaf grows for a time by a two-sided apical cell, from which new cells are cut off right and left in an extremely regular manner (Fig. 57C). In some cases, *e.g.*, in some submerged forms, the cells of the leaf remain practically uniform in size and shape, all containing chloroplasts, but as a rule this condition is rapidly replaced by differentiation of the cells into two sets. Some remain narrow but grow in length, and are arranged so as to form a network, each mesh of which is occupied by a large cell. The narrow cells retain their original contents, the large ones lose their protoplasm and chloroplasts. This differentiation takes place in a remarkably regular fashion. Each cell of the young leaf divides so as eventually to cut off a cell which is directed to the tip of the leaf and another which faces either the right or left side of the leaf; this is shown somewhat diagrammatically in Fig. 57E. where the dotted line represents the central axis of the leaf. The cells facing the apex (A) and the sides (R, L) remain narrow, while the third cell (H) of the triad grows in all directions and forms one of the large hyaline cells (Fig. 57F). As each cell divides in this symmetrical manner we get a regular and beautiful network of

narrow green cells enclosing the large hyaline cells (Fig. 59). The latter have their walls thickened by ring-like bars, which are often joined up; these bars are thickest in the cells of the outstanding

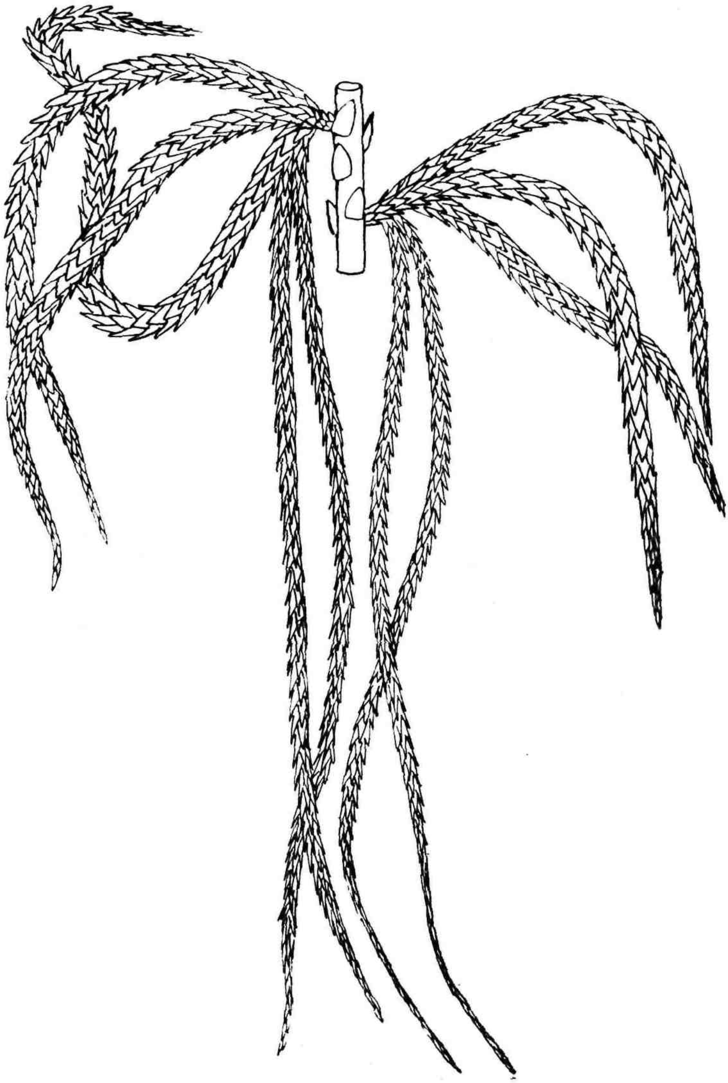

Fig. 56. *Sphagnum acutifolium*. Portion of a plant, showing two of the branch-tufts; in each tuft there are two drooping branches and three outstanding ones.

branches, and their thickness varies considerably according to the habitat, being greatest in plants growing in exposed or sunny places, while the fibres are feebly developed in plants growing in shade or in very wet places, and are often absent altogether in more or less

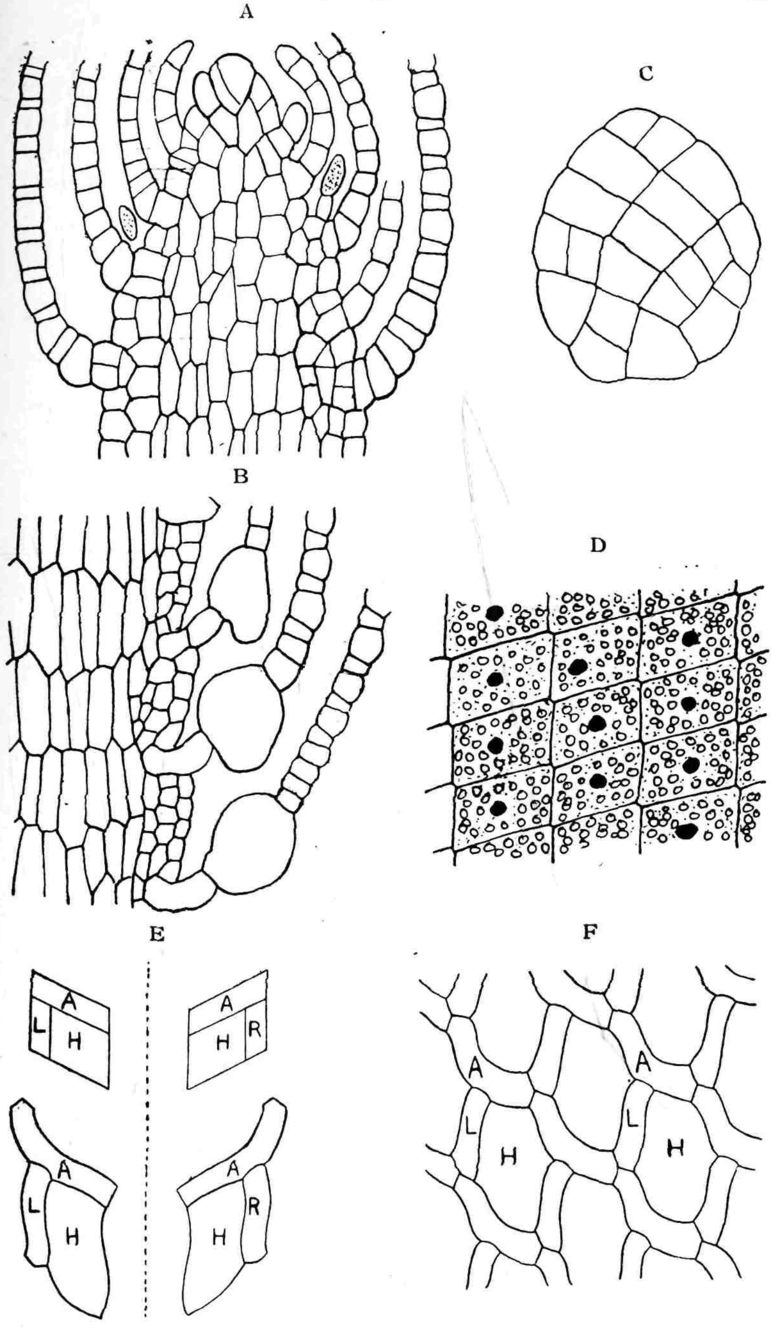

Fig. 57. *Sphagnum acutifolium*. A, median longitudinal section of apex of a stem, showing apical cell; B, similar section at some distance below the apex; C, a young leaf; D, cells from an older leaf; E and F, cells from older leaves, showing the division into triads (see description in text, pp. 2, 3).

submerged plants. In the leaves borne on the main stem, which are soon covered up by the pendent branches and therefore become functionless, the green cells soon lose their chlorophyll, while the walls of the hyaline cells become perforated with holes of irregular size and outline. In the branch-leaves, the hyaline cells have their walls perforated to a smaller extent and in a more regular manner, the pores being circular or oval and having a thickened rim; these pores generally occur at the points where three cells meet, though they are also found along the sides of the hyaline cells where these border on the green cells.

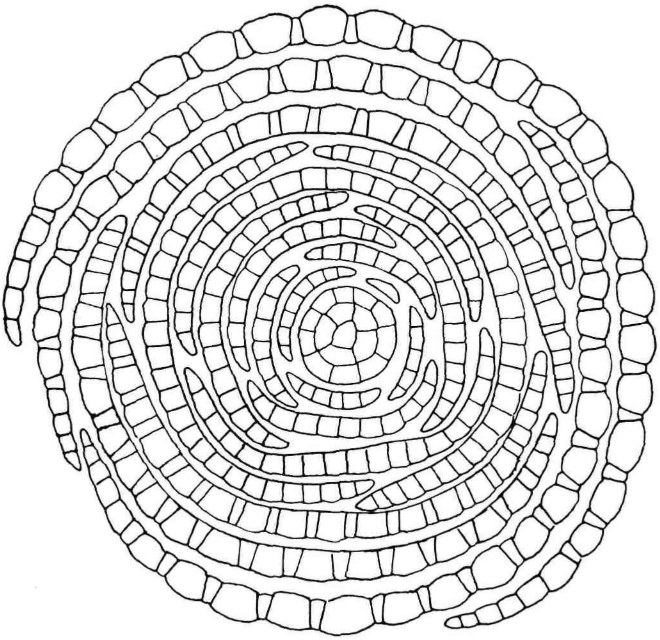

Fig. 58. Transverse section of growing-point of stem of *Sphagnum acutifolium*, showing in centre the apical cell and its youngest segments, and towards the periphery the differentiation of the leaf-cells.

At first a section across a young leaf shows that the cells, arranged in a single layer, are all rectangular and of about the same size, but later the cross-section shows an alternation of large hyaline and smaller green cells (Figs. 58, 59). In some species the hyaline cells bulge towards the underside of the leaf, the green cells being then triangular in cross section with the base of the triangle directed upwards and about flush with the upper side of the leaf. In other species the relation between the two kinds of cells is just the reverse of this; in others, again, the green cells are hemmed in

above and below by the hyaline cells, and may be spindle-like in cross-section, their ends reaching neither the upper nor the lower side of the leaf. The classification of the Sphagna is largely based

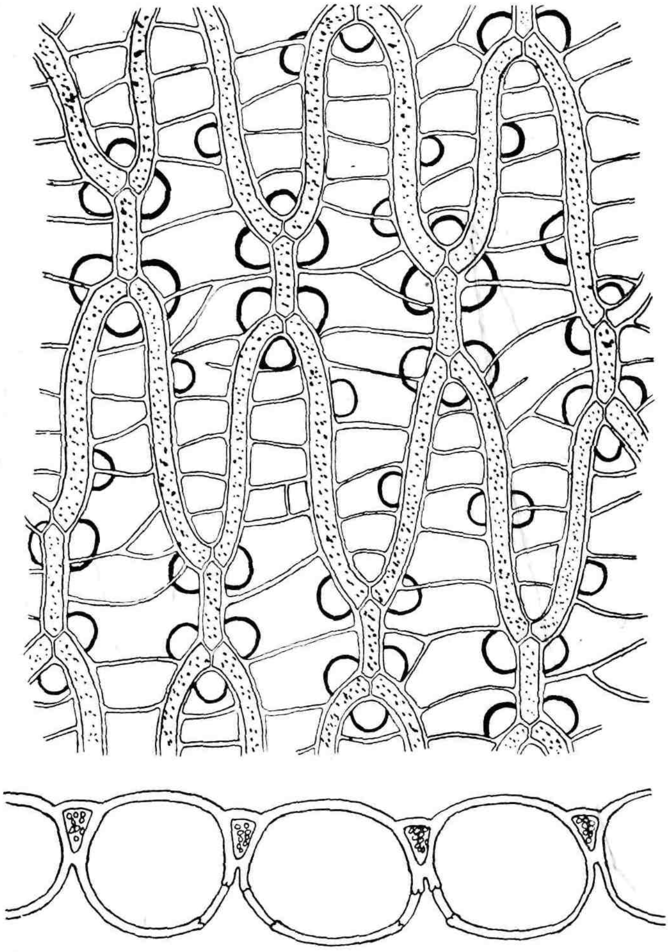

Fig. 59. *Sphagnum acutifolium*; the upper figure shows a portion of a mature leaf in surface view, the lower a portion of a transverse section of the leaf.

on the appearance of the two kinds of leaf-cells as seen in cross-section.

The inner tissue of the main stem consists of long cells sharply separated from an outer zone of short cells (Fig. 57B, Fig. 60). The latter (cortex) is at first a single layer, and in the branches it usually remains one cell thick, but in the main stem it often becomes four layers deep, its cells being large and colourless in

most species. In submerged plants the whole stem consists of uniform tissue, all the cells except the innermost having chloro-

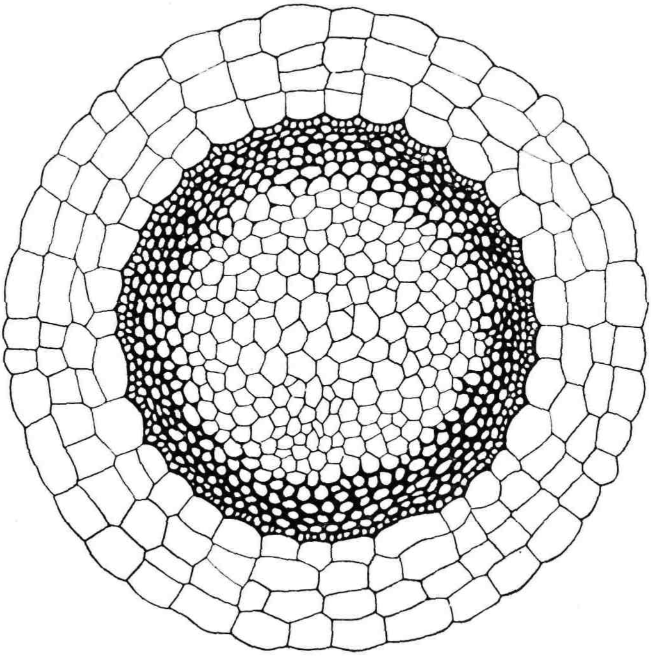

Fig. 60. Transverse section of stem of *Sphagnum acutifolium.*

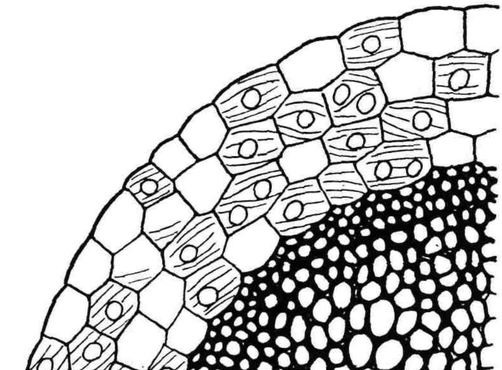

Fig. 61. Transverse section of stem of *Sphagnum cymbifolium.*

plasts—that is, in such plants the stem-tissue undergoes no differentiation and remains in the early stage, which is soon passed

through in plants growing out of water. In a few species (*Sphagna cymbifolia*) the cells of the cortex resemble the hyaline leaf-cells in having strengthening fibres and pores on their walls (Fig. 61), but in most species these cortex cells are devoid of fibres and pores. The tissue within the cortex is differentiated into an outer zone of narrow thick-walled cells and a central region in which the cells are wider and shorter and have thinner walls. In the outer zone the long narrow cells have pits on the walls, but later the walls become uniformly thickened and the pits are obliterated. In the branches, of both the outstanding and the drooping types, some of the cells of the single-layered rind grow large and have their outer wall perforated at the upper end by a circular or oval hole, and as this end often projects outwards these cells resemble a bottle with a curved neck; these "retort-cells," which are especially conspicuous in *S. molluscum* (Fig. 62A), stand at one end of the insertion of a leaf, and they do not occur in the *Cymbifolium*-section, in which the cortex of both the main stems and the branches consists of perforated cells with fibrous thickenings.

Many inaccurate statements are found in text-books concerning the biology of *Sphagnum.* Oltmanns (24) was the first to make careful experiments on the remarkable capacity of *Sphagnum* for absorbing and giving off large quantities of water. In most species, the water is drawn up by capillary action, an extremely effective system of capillary spaces being formed by the drooping branches which hang down against the stem and overlap each other. If the tufts of branches be removed from the end of the stem, which is then dipped into water, the plant remains dry, hence the stem-tissue does not serve a conducting function. But in *S. cymbifolium* and its allies, in which the cortex cells have pores and fibres on the walls, the removal of the pendent branches does not stop the drawing-up of water, though even here water passes up much more rapidly when these branches are left intact; in these species no water ascends at all when both the pendent branches and the cortex are stripped from the end of the stem. As is well known, *Sphagnum* rarely grows on limestone soils. According to Paul (26, 27), calcium carbonate is very injurious to *Sphagnum*, even in small quantities; he grew various species in water containing lime and found that the plants soon perished. He states that not all salts of lime have an equally injurious effect, and that alkaline salts of potassium and sodium are as deleterious as those of lime. Various other writers have stated that the peat-mosses give an acid

reaction on the surface, hence the injurious effects of calcium carbonate may be due to the neutralising of the acidity; that "Hochmoor" forms contain more acid than those growing on "Flachmoor" and that the former are more sensitive to lime; that on "Hochmoor," there is less mineral food available for the Sphagna

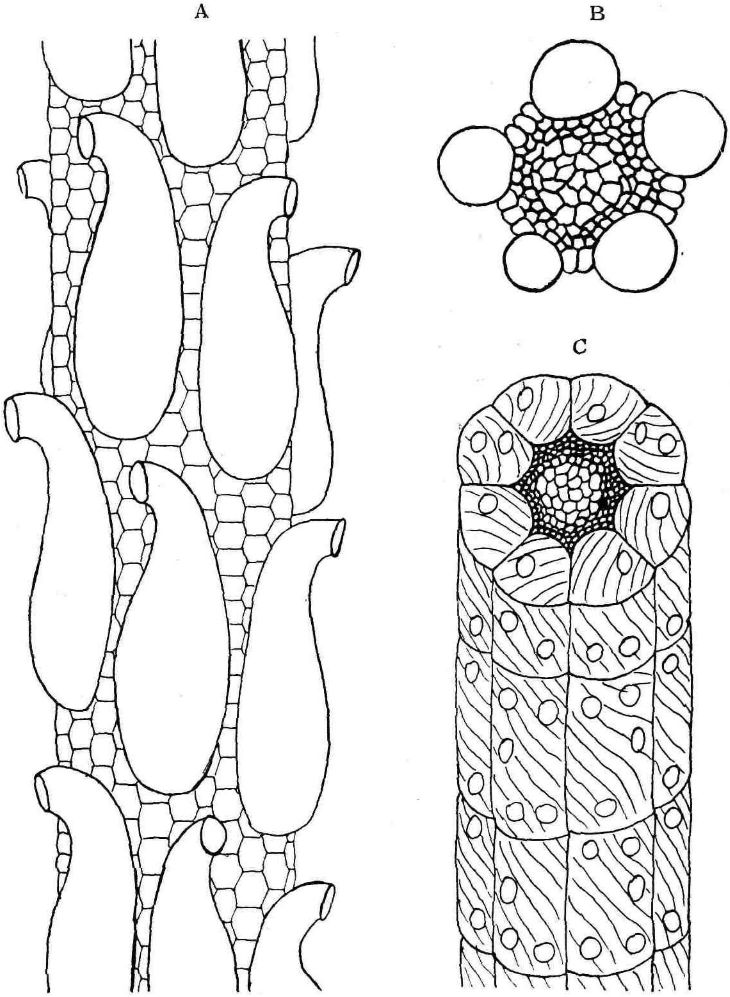

Fig. 62. A, portion of a branch of *S. molluscum*, after removal of leaves; B, transverse section of same; C, portion of a branch of *S. cymbifolium*.

in the sub-stratum, and that the amount of acidity and the sensitiveness to its neutralisation decrease as the amount of available mineral food increases; also that, in general, "Hochmoor" Sphagna absorb more water than "Flachmoor" Sphagna.

Many interesting contributions to the physiology and ecology of *Sphagnum* are to be found in the papers of Peterfi (28), Sernander (46), and Timm (47), besides those of Oltmanns and Paul which have already been referred to; the earlier literature of the subject is given fairly fully by Paul in his 1908 paper. The writer has recently (4) given a summary of some of the more striking features in the biology and ecology of *Sphagnum*.

Since the sexual organs and sporogonium are practically uniform in the various species, the classification of *Sphagnum* is based entirely upon the vegetative organs, and it is at any rate easy to divide the genus into a small number of fairly natural groups, but beyond this point there is no general agreement among sphagnologists, some of whom have carried on controversies quite as spirited and even violent as those which have enlivened the history of lichenology; perhaps the best—or worst—instance is to be found in the wrangle between Röll and Russow regarding the constancy of species in the genus *Sphagnum*, in the course of which Röll called Russow "einen hartgesottenen verbohrten Art-Dogmatiker von der schlimmsten Sorte," and even worse things.

Apart from these somewhat barren and too often polemical discussions, it is generally admitted that the species of *Sphagnum* vary considerably, also that the different sections into which the genus has been divided show analogous variations. As was clearly pointed out by Jensen (8), the variations in the form of the Sphagna may be attributed to differences in the environmental conditions with regard to moisture, light, temperature, etc. The leaves are, naturally, the organs most liable to undergo variation, but the branching is also affected by these different conditions. Jensen distinguished three chief types of "analogous variation":—(i.) "formæ immersæ," growing submerged in water, with long stems, no distinct terminal head—the branch-tufts being widely separated owing to elongation of the stem—and with long leaves, the stem-leaves being similar in structure to the branch-leaves; (ii.) "formæ compactæ," growing in dry or cold habitats, in which the shoots are compact, forming low cushions, the branches short, and the leaves closely overlapping; (iii.) "formæ squarrosæ," growing in sheltered and shaded places, with robust shoots, leaves broad and deep green in colour. Other types are "laxæ," with the leaves widely spaced out; "tenellæ," with unusually long and slender branches and narrow leaves; "falcatæ," with falcate arrangement of the leaves at the curved tips of the branches. Jensen pointed

out that in the *Sphagna acutifolia* and the *Sphagna subsecunda* we get a parallel series of forms showing the various types just mentioned, though the two groups are readily distinguished by the arrangement of the green and hyaline leaf-cells as seen in cross-section; while the *Sphagna cuspidata* and the *Sphagna cymbifolia* contain representatives of about half of the "analogous variation" forms. On the other hand, the *Sphagna compacta* are the least variable types, usually growing in relatively dry places and showing a very limited range of biological forms, nearly all being compact, though squarrose and submerged forms sometimes occur in this group.

The growth of a *Sphagnum* shoot shows a more or less marked annual periodicity, though in winter it is not brought to a standstill unless the temperature falls to freezing point. The laying-down of new branches at the apex proceeds during the whole period of active growth (spring and summer), but the elongation of the stem becomes arrested in late summer or early in autumn. While the stem is lengthening, the outermost (oldest) of the branches forming the cushion-like top of the plant are continually being carried downwards and spaced out in tufts on the stem. Among the later branches formed in autumn are the male and female branches, which may either occur on the same plant or on different plants—most of the British species are diœcious, but some show either condition quite indifferently. The male branches are formed earlier than the female, and are carried down on the stem as the latter elongates, while the female branches arise later and are found during winter and spring on the upper part of the plant, but later are carried downwards as the stem lengthens. The sexual organs usually mature in late autumn and winter, and may be found fully developed in mid-winter, even when the plants are covered by snow. Fertilisation usually occurs in early spring; the young sporogonia may be found as early as February, and the ripe capsules shed the spores from about July to September.

The male branches are at first indistinguishable from the ordinary divergent branches of a tuft, but later they acquire a characteristic appearance. One or more of the branches of a tuft expand and become catkin-like, and above this swollen antheridium-bearing region taper again to a pointed tip which may continue to grow like an ordinary branch, giving the "catkin" a spindle shape. The leaves that protect the antheridia resemble ordinary branch-leaves in structure, but are usually shorter, more closely over-

lapping, arranged in regular straight or spiral rows, and often richly coloured red, purple, brown, etc., even in species where the ordinary branches are devoid of colouration other than pale green. The antheridia are spherical and attached to the axis of the branch by a slender and relatively long stalk which is inserted at one end of the base of the leaf. The position of the antheridia with reference to the leaves is thus the same as that on a branch of a stem, and Leitgeb (10) noticed that a vegetative bud may occupy the place of an antheridium on the male branch, The branching

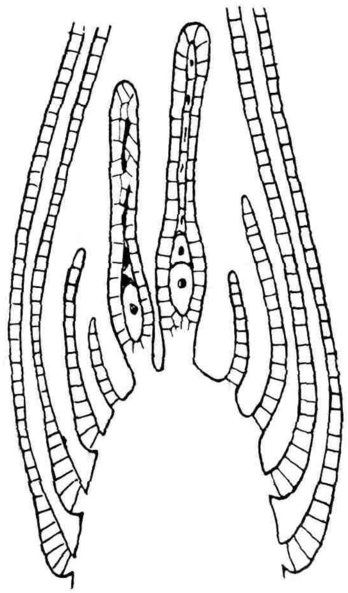

Fig. 63. Longitudinal section of female branch of *S. compactum*, showing two archegonia.

filaments, described by Schimper in his classical work on *Sphagnum* (44) as paraphyses accompanying the antheridia, are only of occasional occurrence, and they probably belong to the fungus which will be mentioned later in connexion with the archegonia and sporogonia. The antheridium arises from a cell which after repeated transverse divisions, producing a cell row, shows apical growth by means of two sets of segments cut from the terminal cell; the lower cells divide longitudinally, as well as transversely, to form the thin stalk.

The female branches are very short and bud-like, deep-green in colour. The leaves externally visible at the top of the branch are usually much longer than any other leaves on the plant; they differ from the branch-leaves in having few fibres in the hyaline

water-cells, and from the stem-leaves in having abundant chlorophyll. The structural peculiarities of these leaves are obviously connected with their functions, the protection and nutrition of the developing sporogonium; owing to the scarcity of fibres in the cells, these leaves closely invest the young fruit instead of being stiff or curved outwards, and their abundant chlorophyll enables them to carry on active photosynthesis. Within the large enveloping leaves we find at the apex of the branch a small group of archegonia surrounded by a number of small leaves which for a long time *remain in* an embryonic or undifferentiated condition (Figs. 63, 64). The first archegonium is formed from the apical cell of the branch, and then from two to four others are developed around it; occasionally there are only two archegonia, or no more

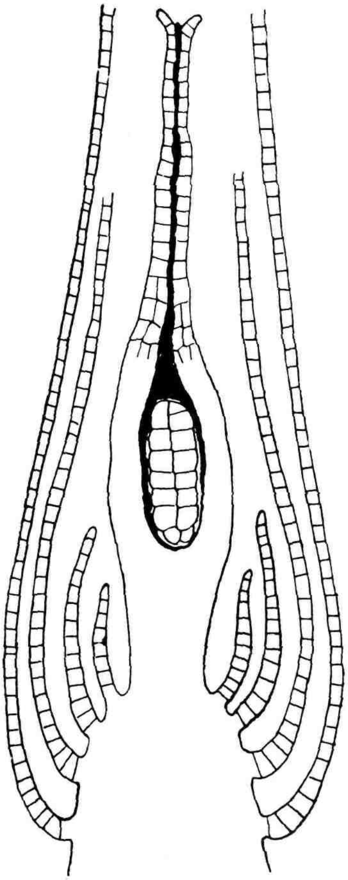

Fig. 64. Longitudinal section of female branch of *S. compactum*, showing fertilised archegonium with embryo.

at all may be produced after the first one. The archegonium resembles that of the Bryales in structure ; it has a thick stalk and the neck-cells are in spiral rows. It has not been determined with certainty whether it grows by means of an apical cell, as in Bryales.

The embryogeny of *Sphagnum* presents some interesting features. The first division of the fertilized egg is into an upper (epibasal) and a lower (hypobasal) cell, but the further development differs from that seen in Bryales and recalls the embryogeny of the Jungermanniales; the hypobasal cell undergoes a few irregular divisions, while the epibasal cell divides repeatedly by transverse

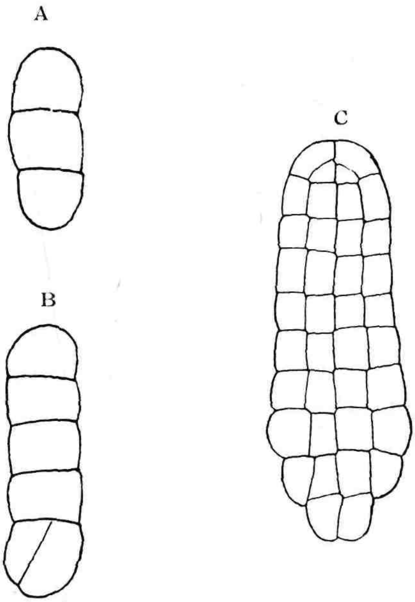

Fig. 65. *Sphagnum compactum.* Three stages in development of embryo sporophyte.

walls to form a row of about six cells (Fig. 65). As in Jungermanniales, each of these cells divides into quadrants and then by tangential divisions a series of inner cells (endothecium) is separated from a layer of outer cells (amphithecium). The embryo soon becomes pear-shaped (Fig. 66), the narrow upper portion eventually producing the capsule, while the lower portion for a time grows much more rapidly and forms the swollen haustorium; at this stage the embryo strikingly resembles that of Anthocerotales, except for the absence of the meristem zone. The archesporium is dome-shaped and arises, as in Anthocerotales,

from the inner layer of the amphithecium, the endothecium of the capsule forming the sterile columella. The archesporium soon becomes four-layered, and the cells adjoining it on both sides divide so as to form a small-celled spore-sac layer, as in Bryales. The stalk of the fertilised archegonium expands as the haustorium bores down into it and into the underlying tissue of the stem, the lower part of the venter also stretching to keep pace with the growth of the capsule, while the withered neck and upper portion of the venter are carried up on the surface of the calyptra.

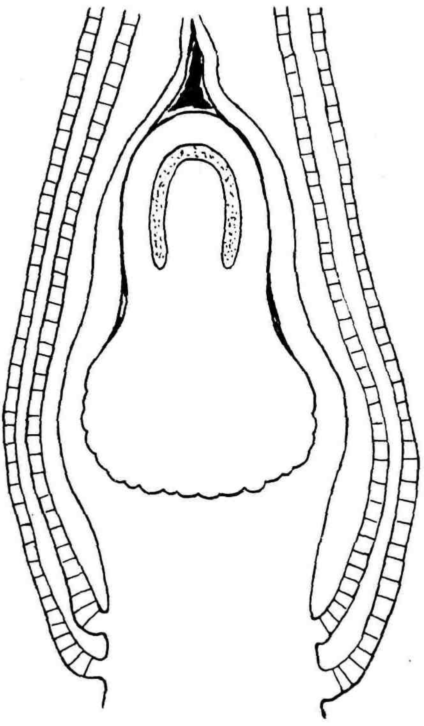

Fig. 66. *Sphagnum compactum*; later stage in development of sporogonium.

Chlorophyll is present in the developing capsule, especially in the tissue lying outside of the spore-sac and in the small cells of the spore-sac itself. As the capsule matures, the cells of the superficial layer acquire thickened and brown coloured walls, forming a well defined epidermis ; along a circular transverse line near the top of the capsule these cells remain small, forming the groove-like annulus and delimiting the lid by which the capsule eventually dehisces (Fig. 67, Fig. 68 c). The epidermis shows numerous rudimentary stomata, which begin to develop like those on the

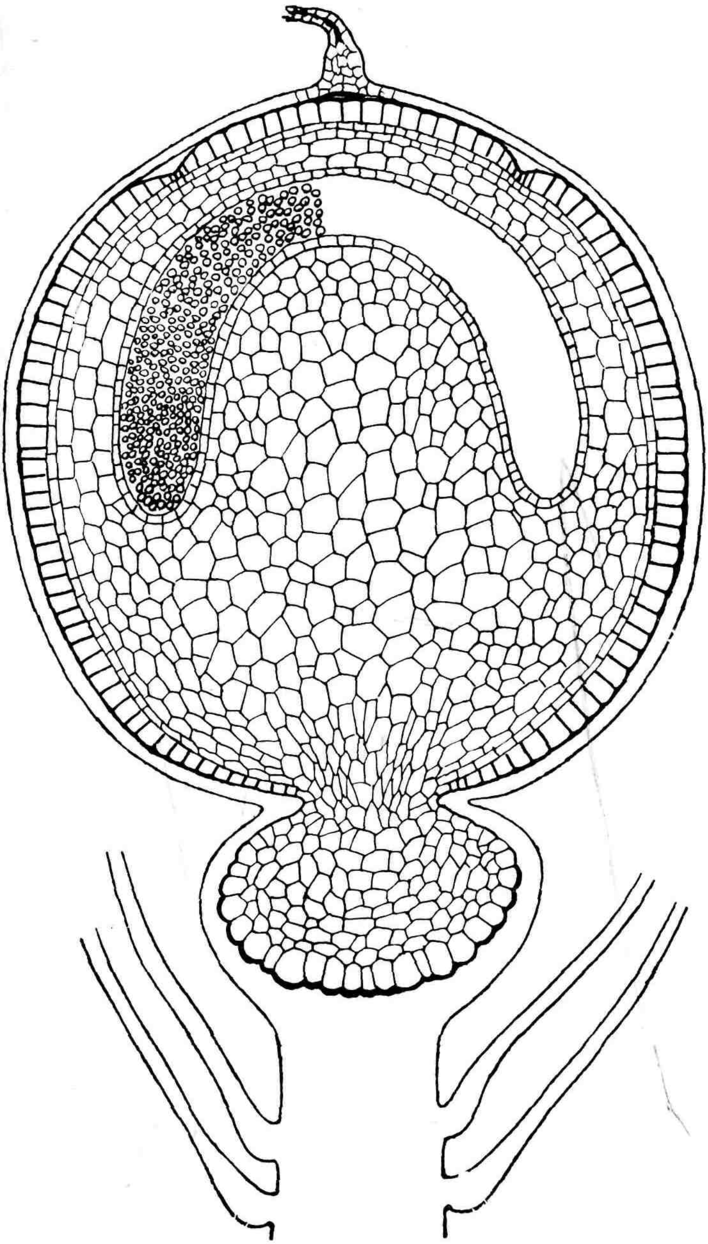

Fig. 67. Longitudinal section of a nearly ripe sporogonium of S. *compactum*. At the top is the withered neck of the archegonium, the lower part (calyptra) of which covers the nearly spherical capsule. The capsule-wall shows the groove which separates off the lid. The dome-like spore-sac (spores only shown on left side), and the central tissue (columella) are seen. The capsule is connected by a constriction with the absorbing foot. Elongation of the pseudopodium has not yet taken place.

apophysis of many Bryales, an isolated epidermal cell remaining thin-walled and dividing into two "guard-cells," but the partition-wall not splitting to form a pore (Fig. 68 A, B.) The ripe capsule is raised on a "pseudopodium," formed by elongation of the upper part of the axis of the female branch, the uppermost leaves of which become slightly separated, though the growth is greatest between these leaves and the sporogonium itself, so that the pseudopodium has a smooth surface and consists of elongated cells; the top of this apparent seta is occupied by the bulbous

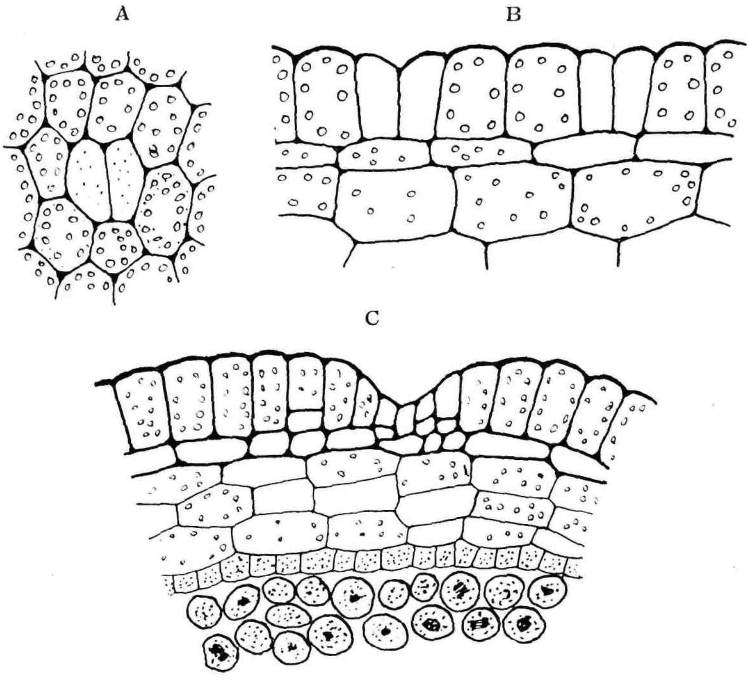

Fig. 68. *Sphagnum acutifolium.* A, stoma in surface view; B, part of longitudinal section of capsule, showing two stomata; C, part of longitudinal section showing the annulus and part of the spore-sac, with developing spores.

haustorium, which is separated from the capsule by a neck consisting of narrow pitted cells. The calyptra is ruptured irregularly by the slight expansion of the ripening capsule; leaving a cup-like sheath; sometimes the rupture is transverse, so that the upper portion of the calyptra is pushed up like a cap, tipped by the archegonium neck, on the top of the capsule.

Among the archegonia, as well as the antheridia, branching filaments sometimes occur, which were regarded by Schimper as paraphyses serving to keep the sexual organs moist. Doubt was

thrown upon this observation by Leitgeb (8), who investigated the development of the antheridia, and by Waldner (49), who worked out the embryology of the sporogonium; in fact, neither of these writers could observe such threads at all. Schimper and other observers also noticed that the capsule sometimes contains very small spores which to a greater or less extent replace the ordinary spores. Schimper described these "microspores" as arising from the ordinary spores by repeated division, and Warnstorf suggested that *Sphagnum* is a heterosporous Bryophyte, the microspores producing male plants and the large spores female plants! However, Nawaschin (20, 21) showed that the filaments and the "microspores" belong to a parasitic Fungus—*Tilletia Sphagni*—the life history of which he worked out, tracing the entrance of the mycelium into the developing capsule and its ramification through the archesporium, where it produces its own spores, mingled with those of *Sphagnum* or even, in small and deformed capsules, replacing them altogether.

The dehiscence of the capsule is brought about by a curious and probably unique mechanism. It was long ago noticed that the capsule of *Sphagnum* explodes with a cracking or "popping" noise, the shape of the capsule suddenly changing from spherical to cylindrical, and the lid, together with the spores, being thrown out to a distance of several inches. The beautiful mechanism involved was explained by Nawaschin (22). As the ripe capsule dries, the delicate central tissue (columella) shrivels and is replaced by air, so that the capsule eventually contains, within the brown epidermal ayer, practically nothing except the spore-sac (by this time an inverted saucer-like bag within which the spores lie loosely) and below this a relatively large air cavity. As drying proceeds, the longitudinal diameter of the capsule remains unchanged, but the transverse diameter is greatly shortened owing to transverse contraction of the epidermis, and the imprisoned air is therefore compressed. During this change, the lid (firmer in texture than the rest of the wall) shrinks but little, a difference in tension is thus set up, and finally the lid becomes loosened along the annular groove and is forcibly shot off, along with the spores, in exactly the same way as a bullet from an air-gun. Nawaschin's paper (22), should be consulted for details of his ingenious experiments and his determination of the volume and pressure of the air in this remarkable "pop-gun" capsule.

The protonema of *Sphagnum* differs from that of most other

Mosses. The germ-tube given out by the spore is soon converted, by growth of its end-cells, into a flat discoid thallus, forming an irregularly lobed expansion one cell in thickness, attached by numerous rhizoids. The protonema may reproduce itself by sending out from its margin threads which give rise to discs, and these may later become separated as independent protonemata. Usually one leafy *Sphagnum* plant arises from each protonema, as a projection formed by active growth and division of a marginal cell at the base of the protonema; in this cell arise walls cutting out a three-sided apical cell, the segments cut out from this at once producing the young leaves. The fourth or fifth leaf shows the differentiation into green and hyaline cells; at first this differentiation is shown only in the lower portion of the leaf, the upper cells remaining uniform and green.

Oehlmann (23) has shown that *Sphagnum* plants are able to produce protonemata and young leafy plants from practically any living portion of the mature gametophyte. The young *Sphagnum* plant, whether arising from primary protonema (produced on germination of the spore) or from secondary protonema (in regeneration of portions of the mature plant) bears rhizoids which may twine like tendrils around old *Sphagnum* stems and other supports; but as the plant developes it produces no more rhizoids, these absorbing hairs being unnecessary since the plant has such efficient means of absorbing water in its remarkable capillary system and its perforated hyaline cells.

The affinities of *Sphagnum* will be discussed later, when the characters of the Andreæales and Bryales have been dealt with.

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VII. ANDREÆALES.

THIS group is represented by the single genus *Andreæa*, which is in various respects intermediate between the Sphagnales and the Bryales, especially in the structure and development of the sporogonium. There are about 100 species of *Andreæa* distributed over the whole earth, but especially abundant in the colder temperate regions, though found on the higher mountains in the tropics. They are small plants, which creep and branch sympodially, forming dark brown or black tufts, and growing especially on siliceous rocks in exposed places—though two New Zealand species grow on wet stones in streams.

The mature stem and leaf hardly differ in structure from those of various Bryales. The stem tissue is practically uniform, there is no definite conducting strand ; the leaf usually consists of a single layer of cells, but in some species has a midrib. From the basal creeping portions of the stem there spring numerous rhizoids, mostly consisting of cylindrical or plate-like outgrowths, the former growing into the rock crevices, while the latter become applied closely to the rock surface.

The sexual organs are borne in terminal groups on separate branches, usually on the same plant ; each group is surrounded by a number of large involucral leaves, and among the antheridia and archegonia there are numerous filamentous paraphyses. The development of the sexual organs was worked out by Kühn in his fine memoir on the genus (3), and apparently *Andreæa* shows close resemblance to the Bryales in the general characters of these organs. The mature antheridium has an ellipsoid body and a relatively long stalk, the latter consisting of two rows of cells and having a dilated base.

The sporogonium of *Andreæa* presents a curious mixture of characters, some of which are peculiar to the genus, while others recall the structural and embryological features of the sporophytes of Sphagnales and of Bryales. After the formation of the transverse basal wall, the divisions in the hypobasal cell are irregular, but the epibasal cell divides at once by oblique walls which cut out a two-sided apical cell. According to Waldner (4), who worked out the early stages in detail, the apical cell cuts off, as a rule, about six segments on either side before further divisions occur in the

segments. Each segment is first divided by a radial wall, and then tangential walls are formed which separate a central group (endothecium) of four cells from an outer layer (amphithecium) of eight cells, as seen in cross section of the embryo. In the upper segments—beginning with third oldest, and extending through three or four segments above this one—the archesporium is formed as a layer of cells cut from the endothecium, the central portion of which forms the columella, while the ampithecium gives rise to the capsule-wall. The archesporium becomes two-layered, and is dome-shaped, extending over the top of the columella, as in *Sphagnum*. The two lowest epibasal segments contribute to the foot; those above the archesporium produce the sterile tip of the capsule (see Fig. 69, A to J).

The ripe capsule is ovoid in form, having a very short seta or neck connecting it below with the somewhat swollen foot or haustorium. The capsule-wall consists of about six layers of cells, at first containing chloroplasts; the epidermal cells are thick-walled over the greater part of the capsule, but along four longitudinal lines which are equidistant from each other and reach neither the apex nor the base of the capsule—these lines are laid down at a very early stage and doubtless correspond to the primary quadrant divisions in the archesporium-forming cells of the embryo—the epidermis cells have thin walls and divide tangentially so as to form two superposed rows (Fig. 69, M, N).

The venter of the fertilised archegonium grows actively, forming the calyptra and becoming about six cells thick; after a time, when the capsule is nearly mature, the calyptra is ruptured and its upper portion is carried up on the apex of the capsule. As in *Sphagnum*, the axis of the archegonial shoot grows up as a psuedopodium, carrying on its surface some of the unfertilised archegonia, and expands above into a swelling in which the sporogonial haustorium is embedded (Fig. 69, K, L). When the ripe capsule dries, dehiscence occurs along the four longitudinal lines marked out by the rows of thin-walled epidermis cells already

Fig. 69. *Andreæa*. A to C, stages in development of the embryo sporophyte, in longitudinal section; F to J, similar stages in transverse section; K, diagrammatic view of the entire sporogonium after elongation of pseudopodium and transverse rupture of the venter of the fertilised archegonium; C, longitudinal section of fairly advanced sporogonium, showing the archesporium, calyptra, and vaginula, also the upper portion of the pseudopodium in which is inserted the foot of the sporogonium; M, part of a transverse section of a fairly advanced sporogonium, showing one of the dehiscence lines in the epidermis of the capsule-cell; N, similar section of a ripe sporogonium. All the figures are somewhat diagrammatic; *c.*, *col.*, columella; *cal.*, calyptra; *e.*, endothecium; *d. l.*, dehiscence line; *sp. s.*, spore-sac.

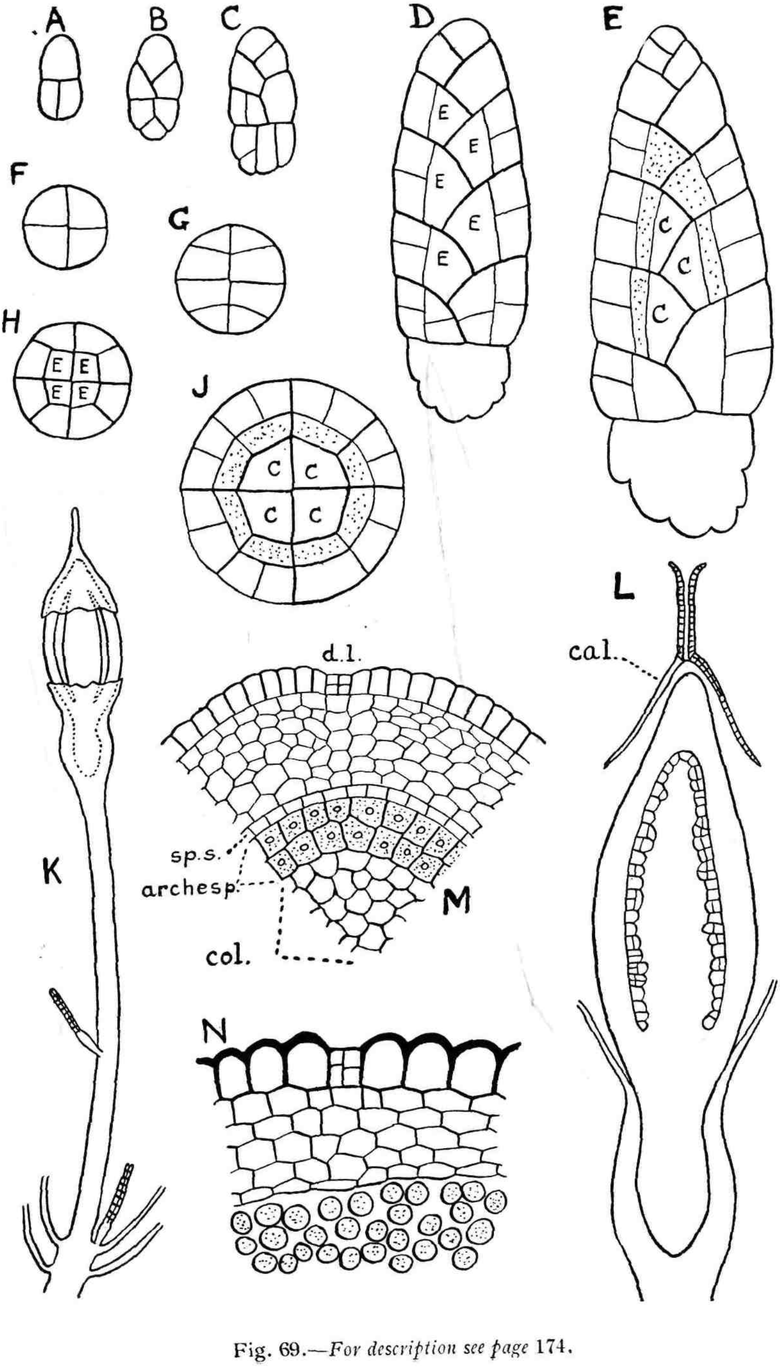

Fig. 69.—*For description see page* 174.

noted. In most cases the capsule opens by four slits, extending neither to apex nor base of capsule, but in some species there are from six to eight slits; while in *A. Wilsonii* (a South American species) the capsule is said to open by slits that reach the apex and extend only a short distance downwards, so that the whole tip of the capsule splits into from four to eight teeth. Unfortunately, the species just named has not been fully investigated; careful examination of fresh or suitably preserved material would be of great interest, in order to determine whether or not we have here a transition from the peculiar dehiscence mechanism of the typical Andreæales to that seen in *Tetraphis*. As shown by Goebel (2), the moist spores adhere to the edges of the slits, which close in wet weather, and become dry and loosened when the slits gape on drying.

The germination of the spores and the peculiar forms of the protonema were investigated by Kühn and also by Berggren (1). The spore begins to germinate and forms a cell-mass before the exospore is ruptured; when rupture occurs, the superficial cells of the mass grow out separately to form filaments which grow apically, segments being cut off from the terminal cell by transverse walls. These filaments branch freely, some of the branches creeping over the substratum, while others grow upwards and turn green, others again growing into crevices in the rock and remaining colourless. The erect filaments may become cylindrical and produce flat leaf-like plates, hence the forms of the protonema are very diverse, and any of them may produce buds which grow into leafy shoots. Elaborate protonemata of a very similar kind occur, however, in various Bryales.

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VIII. BRYALES.

OMITTING for the present the vegetative characters, the three groups of higher Bryophytes or Mosses may be thus distinguished:—

I. **Sphagnales.** Embryo sporophyte first divides into a row of several cells, by formation of repeated transverse walls in the epibasal cell; haustorium formed by growth and division of hypobasal cell; further growth of epibasal half intercalary; archesporium produced chiefly from the innermost layer of the amphithecium; the endothecium forms only the columella, except at the apex, where it contributes to the production of the dome-like archesporium; mature sporogonium consists of a spherical capsule and a bulbous haustorium, the two being separated by a constriction: capsule carried upwards by elongation of female shoot axis to form a pseudopodium, and opening by a lid.

II. **Andreæales.** Epibasal cell divides by inclined walls cutting out a two-sided apical cell, by which growth is effected for some time (until the differentiation of the archesporium); hypobasal cell divides irregularly; haustorium formed by hypobasal half and lowest segments of epibasal half; archesporium produced chiefly by the outermost layer of the endothecium, the inner portion of which forms a columella; archesporium dome-shaped, being completed above by the inner tissue of the endothecium, and therefore covering the apex of the rod-like columella; mature sporogonium carried upwards by a pseudopodium; capsule opens by four longitudinal slits, which typically reach neither apex nor base of capsule.

III. **Bryales.** Epibasal and hypobasal halves of embryo usually both grow by a two-sided apical cell; the haustorium, separated from the capsule by a longer or shorter seta, is developed chiefly from epibasal cell; archesporium arises in the outermost

layer of the endothecium (in *Archidium* from the entire endothecial tissue) and is a tubular zone, hence the columella extends into the apex of the capsule; ripe capsule usually opens by a lid, which in the higher types is detached by the separation of a ring of special cells and not merely by splitting of cell-walls, and a special mechanism (peristome), which ensures gradual spore-dispersal, is usually present and is typically developed from the inner amphithecial tissue lying above the archesporial region of the capsule.

These three groups are closely connected with each other, and sharply separated in many respects from the lower Bryophytes. The three "Moss" groups agree closely in the vegetative characters of the gametophyte, in the growth of the young archegonium by means of an apical cell, and in the absence of sterile cells or elaters from the archesporium.

The Bryales, by far the largest group of Bryophyta, present extraordinary uniformity in the early development of the sporogonium and the mode of origin of the sporogenous tissue. Comparatively little work has been done on the embryogeny of the group, but it would appear that in general the archesporium arises from the outermost zone of the endothecium, and the outer spore-sac from the innermost zone of the amphithecium, the characteristic air-space of the Bryinean capsule being formed between the outer amphithecial tissue (which produces the capsule-wall) and the outer spore-sac, while the inner spore-sac consists of a layer of cells cut off from the inner side of the primary archesporial layer. The only outstanding exception to this general and probably universal mode of origin of the sporogenous tissue is that seen in the genus *Archidium*; here the air-space is formed as in typical Bryales, but there is no definite archesporium, unless we regard the entire endothecium as representing the archesporium; at any rate, there is no differentiation into columella and archesporium proper, and a few of the endothecial cells become spore-mother-cells, the sterile cells among which the fertile cells are scattered being absorbed during the maturation of the spores. In *Ephemerum* the embryogeny follows the normal Bryinean type, but the central sterile tissue of the endothecium produces a relatively feeble columella, which in some species disappears before the capsule reaches maturity. In the allied genus *Nanomitrium*, the slender columella is used up in the ripening of the spores, but the capsule has a zone of cells which form a rudimentary annulus and delimit the upper portion of the capsule as an operculum.

The primary division of the Higher Mosses into Cleistocarpi (capsule opening by irregular rupture or by decay of its wall) and Stegocarpi (capsule opening by a predetermined dehiscence line or zone which throws off the apical portion of the wall as a lid or operculum) appears to have been first proposed by Müller in 1849, and it has been maintained by the majority of bryologists to the present day, as has also the division of the Stegocarpi into Acrocarpi and Pleurocarpi (according to the position of the archegonial group, and therefore of the sporogonium, at the end of the main axis or that of a short lateral branch) which was made by Bridel in 1826. On various grounds, neither of these distinctions can now be regarded as forming a sound basis for the classification and phylogeny of the Bryales. Lindberg in 1879 distributed the cleistocarpous forms among the various stegocarpous families, to which he attached them according to their general resemblances apart from the absence of a lid. The cleistocarpous Bryales are mostly very small plants, often with the protonema persistent and more conspicuous than the leafy gametophyte and with the seta short or almost absent; the capsule wall at maturity consists usually of a single layer of cells, though (except in *Nanomitrium*) bearing stomata; and in some of the forms placed in this group there is a rudimentary annulus (*Nanomitrium*) and even a rudimentary peristome (*Mildeella*), though in the latter case this organ is functionless, since the rudimentary operculum does not become detached. Excepting *Archidium*, such of these cleistocarpous types as have been investigated (*Ephemerum*, *Pleuridium*, *Phascum*, *Nanomitrium*) show the typical Bryinean embryogeny. Much more detailed work on the cleistocarpous forms appears to be required before one can venture an opinion on the vexed question whether they are primitive forms, lying at the starting-point of several lines of development leading up to the typical Bryales, or on the other hand degenerate forms derived by reduction from various distinct groups of the stegocarpous Bryales.

The old distinction into Acrocarpi and Pleurocarpi must be abandoned, for many reasons. Many pleurocarpous forms occur among such acrocarpous families and genera as Leucobryaceæ, *Fissidens*, *Pleuroweisia*, etc.; not only do different species of the same genus differ in this respect, but in some cases the same plant may be both pleurocarpous and acrocarpous, *e.g.*, species of *Daltonia*, *Fissidens*, *Hypopterygium*. The division of the stegocarpous Bryales into Acrocarpi and Pleurocarpi is not only quite artificial, but it com-

pletely obscures the phylogeny of the group, for there can be no doubt that the pleurocarpous forms have arisen independently from various acrocarpous groups—a line may be traced, for instance, from the acrocarpous Orthotrichaceæ through intermediate forms like the Hedwigiaceæ and Cryphæaceæ to such typically pleurocarpous forms as *Eurhynchium* and *Hylocomium*, while another line leads upwards from the Bartramiaceæ to the Spiridentaceæ. Moreover, the characters of the peristome are practically identical in detail, as well as in the general structural plan, in such families as the Bryaceæ and Hypnaceæ, which, on the generally accepted classification, are widely removed from each other.

The most striking feature in the organisation is the evolution of the peristome, and it is upon the characters of this organ that something approaching a natural classification must be founded. Here again much remains to be done on the developmental side, for there are many gaps in our knowledge of the origin of the peristome and the annulus, despite the excellent memoirs of Lantzius-Beninga, Philibert, Goebel, Dihm, and others. Moreover, as pointed out by Loeske (31) in his recent interesting book on the Morphology and Classification of Mosses, welcome aid in the attempt to trace out the main lines in the evolution of the Bryales may come from practically every piece of research undertaken on the histology, physiology, and ecology of the various families, and there is room for careful monographs of many of the orders and genera.

Detailed treatment of the Bryales would unduly extend the scope of the present series of articles, and must therefore be left over for another occasion, but in order to draw together some of the more important results of recent work a brief summary will be given regarding the phylogeny of the Bryales. In this group we can distinguish four sharply marked types of peristome-structure, upon which it is probably justifiable to split up the higher Mosses into four independent series co-ordinate with the Sphagnales and Andreæales. The division suggested here is a compromise between the systems recently proposed by Lorch (32) in his fine monograph of the Polytrichaceæ, and by Fleischer (14) in his great work on the Mosses of Java. According to Lorch, the Bryales should be

Fig. 70.—*Tetraphis pellucida.* I. Upper portion of ripe capsule, with four peristome teeth; above is the detached operculum. II. Transverse section of young capsule, taken above the annulus; the four central cells (columella portion of the operculum) have already split apart. III. Transverse section of upper portion of nearly ripe capsule; the outermost layer of cells forms the operculum. IV. Transverse section of operculum and peristome of ripe capsule. in which the operculum has become loosened and the four teeth have split apart. II. and III. from Goebel.

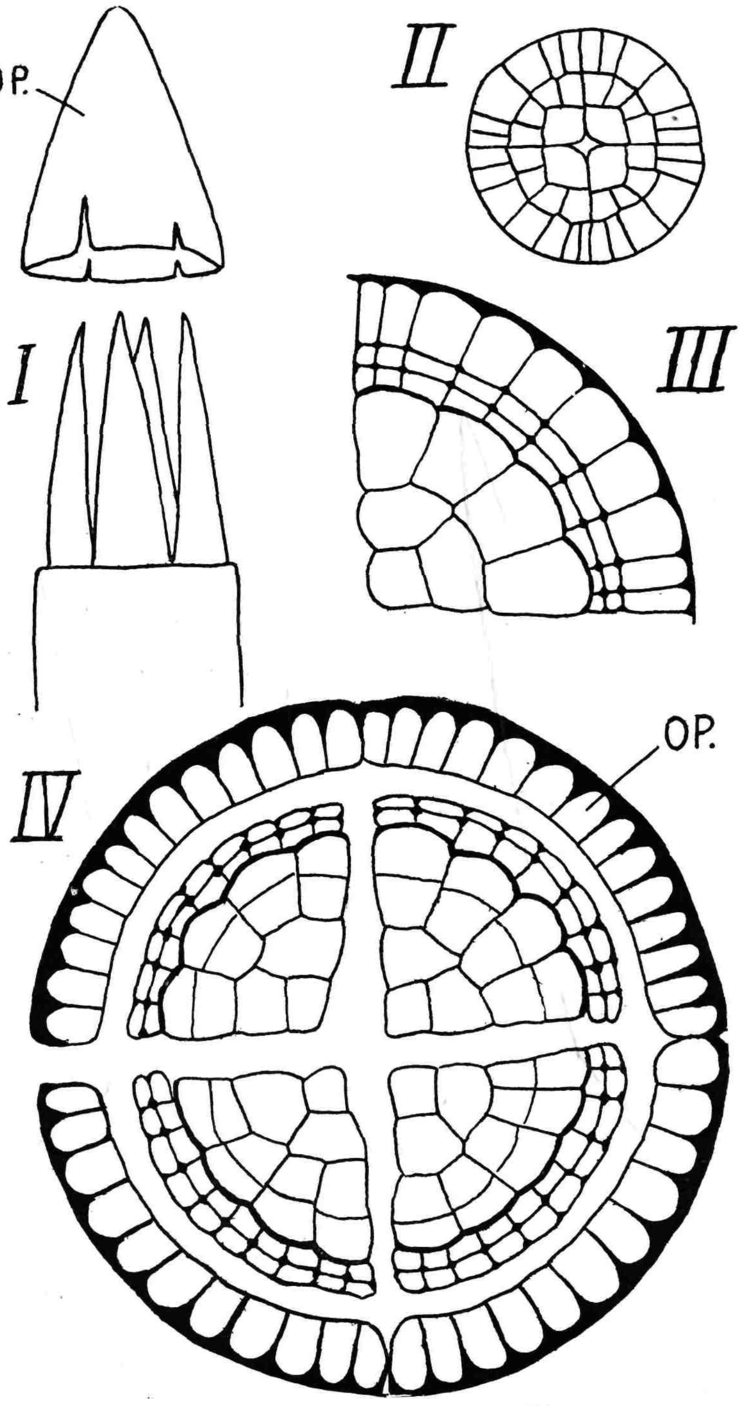

Fig. 70.—*For description see page 180.*

broken up into the four groups Polytrichales (Polytrichaceæ and Dawsoniaceæ), Buxbaumiales (*Buxbaumia*), Diphysciales (*Diphyscium*), and Bryales (or Eu-Bryales). Fleischer, on the other hand, unites the Buxbaumiaceæ and Diphysciaceæ into one group (Buxbaumiineæ), and splits off the Tetraphidaceæ as a second group (Tetraphidineæ), the Polytrichaceæ and Dawsoniaceæ as a third (Polytrichineæ), the remaining Bryales being placed in his group Eu-Bryineæ. It would seem better to raise Fleischer's sub-groups of Bryales into independent groups—Tetraphidales, Polytrichales, Buxbaumiales, and Eu-Bryales. These groups may be briefly characterised as follows:—

I. **Tetraphidales.** Peristome consists of four solid pyramidal cell-masses, formed by the splitting, along two intersecting radial planes, of the entire tissue lying within the single-layered lid (operculum) of the capsule. The group comprises two orders—Tetraphidaceæ with the genera *Tetraphis* and *Tetradontium* and Calomniaceæ with the genus *Calomnium* (with a single tropical epiphytic species). *Calomnium* has no peristome, but otherwise it closely resembles *Tetraphis*; for instance, its rhizoids, which grow on the aerial roots and stems of Ferns, produce erect branched leaf-like assimilating organs similar to those borne on the protonema of *Tetraphis*.

The peculiar and probably primitive peristome of *Tetraphis* may in some respects be compared with the elaterophore of *Aneura* and *Metzgeria* among the Jungermanniales, since the four intersecting cleavage lines appear in the apical tissue of the capsule at an early stage in development (see Fig. 70).

II. **Polytrichales.** Peristome arises in the inner zone of the amphithecium, consisting of a variable number of cell-layers,

Fig. 71.—*Dawsonia.* I. Upper portion of capsule, with peristome of numerous bristle-like processes. II. Transverse section of upper portion of young capsule, showing the relatively broad peristome-forming zone. II. A portion of III, magnified to show the narrow thick-walled cells and the wide thin-walled cells of the peristome zone—the former produce the peristome teeth, the latter break down; outside of the peristome zone is a layer of thin-walled tissue, which breaks down when the operculum becomes detached. IV and V. Diagrams showing the origin of the peristome processes (B) as small cells cut from the cells of the peristome zone, the remainder of each cell (A) being thin-walled and eventually breaking down. VI. Part of a longitudinal section of young capsule, showing the narrow peristome cells (B) and the intermingled thin-walled cells (A). VII. A portion of a peristome tooth consisting of two rows of thick-walled cells. VIII. Longitudinal section of upper portion of nearly ripe capsule. IX. A portion of VIII, magnified highly. X. Detached operculum, cut longitudinally, to show the rod-like columella tissue which comes off with the outer cone-like tissue of the cap. *A.s.*, air space; *ann.*, annulus; *col.*, columella; *op.*, operculum; *per.*, peristome; *sp. s.*, spore sac. Except I., all the figures are from Goebel, but made somewhat diagrammatic.

and the teeth (typically U-shaped at the base) are formed from entire cells arranged in rows or bundles. In *Dawsonia* the

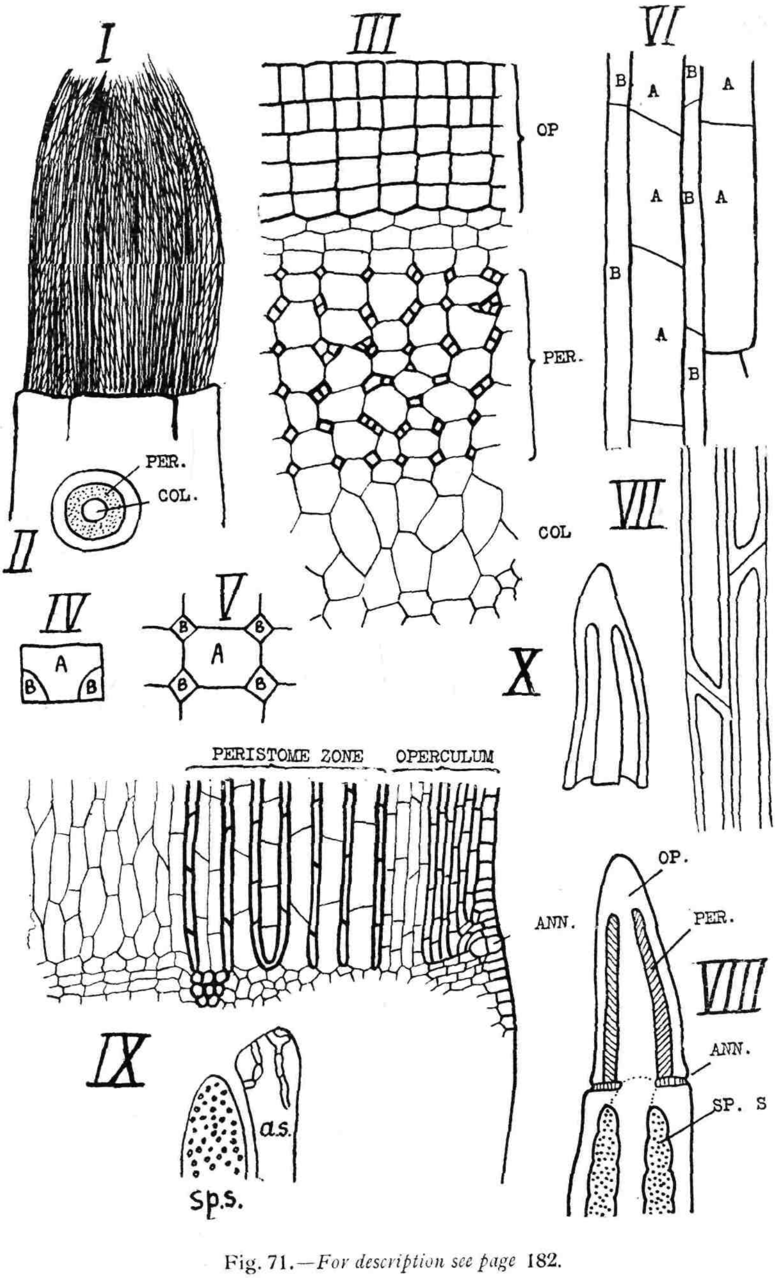

Fig. 71.—*For description see page* 182.

peristome-forming zone is broad, and the peristome consists of numerous long filaments (single cell-rows or bundles of cell-rows) which become separated by resorption of the intervening thin-walled tissue of this zone. In Polytrichaceæ the *peristome arises from* a single annular series of cells, in which curved dividing walls appear in such a way as to form bundles constituting a ring of thirty-two or sixty-four (rarely sixteen) short pyramidal teeth; the tips of these are joined to a thin membrane (epiphragm) formed by the basal tissue of the columella in the operculum, and a poppy-like mechanism results from resorption of the uppermost curved cells between the tips of the teeth (see Figs. 71, 72).

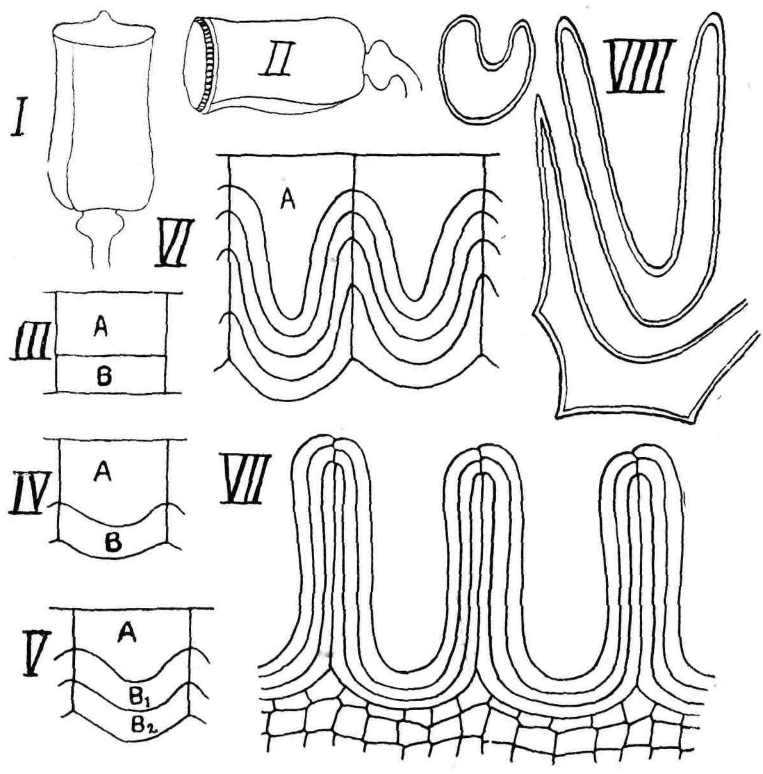

Fig. 72.—*Polytrichum*. I. Ripe capsule. II. Capsule after curvature of the seta and dehiscence of the operculum. III to VI, Diagrammatic tangential sections of the peristome-forming layer, showing the divisions which cut out the peristome-forming cells (B) from the thin-walled upper cell which becomes disorganised to form the pore between two adjacent peristome teeth. VII, three peristome teeth, each consisting of a bundle of cells. VIII, three cells isolated by maceration from a peristome tooth. III to VI and VIII from Goebel.

III. **Buxbaumiales.** Peristome double, arising in several (three to six) *concentric cell layers* of the amphithecium. Outer peristome (exostome) consists of from one to four series of slender teeth, the inner peristome (endostome) of a thin tubular membrane resembling a truncated cone and showing sixteen or thirty-two longitudinal folds. Both peristomes consist of thickened cell-walls only, not of entire cells, as in Tetraphidales and Polytrichales. In this respect the Buxbaumiales approach the Eu-Bryales, though the greatest distinction between the two groups lies in the fact that in Eu-Bryales the number of layers constituting the peristome-forming zone is more definitely limited.

IV. **Eu-Bryales.** Here the peristome-forming zone consists either of two or three layers of cells, the walls of which become *thickened in such a way as to form* typically flat triangular teeth, the unthickened walls becoming resorbed, so that the teeth consist of plates representing the thickened portions of the walls of either two or three concentric cell-layers. The horizontal walls in some cases do not undergo complete resorption, so that the teeth are then chambered and appear in longitudinal section to consist of a row of cells, though these cells are open at either side of the tooth. The number of teeth is typically either sixteen or thirty-two, more rarely eight or sixty-four. Where resorption is incomplete (e.g., *Splachnum*, *Splachnobryum*, *Leptostomum*, *Leucodon*) the peristome is regarded as being in reality double, and it is an open question whether this "chambered" type of peristome is primitive or reduced. The Eu-Bryales are sub-divided, on the peristome structure, into three series.

(A). *Haplolepideæ.* Here the peristome consists of a single series of teeth, formed of membranes belonging to two concentric cell-layers. The outer face of each tooth shows a single row of membranes, while the inner face shows two series of membranes owing to the presence of the remains of the radial walls of the inner peristome-forming layer of cells. The sixteen teeth are either simple or are divided more or less deeply into two (sometimes three) lobes or filaments. The Haplolepideæ are divided into five cohorts, differing with regard to the entire or lobed character of the teeth, the presence or absence of a collar-like "properistome" outside of the peristome, the relative thickness of the two membrane layers composing each tooth, the presence or absence of striations and papillæ on the outer and inner faces of the teeth, the presence or

absence of a basal membrane to which the teeth may be joined below, etc. (i.) *Archidioideæ*, with the single genus *Archidium*. (ii.) *Dicranoideæ*. Teeth usually cleft into two or rarely three lobes, outer layer with longitudinal striations and thinner than the inner layer, which has more or less distinct transverse bars, no basal membrane, no properistome. Families:—Dicranaceæ, Fissidentaceæ, Leucobryaceæ. (iii.) *Monocranoideæ*. Teeth undivided, outer layer with papillæ, the two layers of about equal thickness, no basal membrane, properistome often present. Families:—Leucophanaceæ, Syrrhopodontaceæ, Calymperaceæ. (iv.) *Ditrichocranoideæ*. Teeth usually divided deeply into two or rarely three filamentous lobes, usually with papillæ, transverse bars feebly developed, basal membrane usually present, no properistome. Families:—Trematodontaceæ, Angstrœmiaceæ, Ditrichaceæ, Trichostomaceæ. (v.) *Platycranoideæ*. Teeth broad and thin, undivided or perforated by slits—more rarely split into two or three lobes, outer teeth thicker than inner, no basal membrane, properistome sometimes present. Families:—Seligeriaceæ, Grimmiaceæ,

(B). *Heterolepideæ*. In the single small family placed here (Encalyptaceæ) the calyptra differs from that of other Bryales by its relatively large size and long-continued growth and persistence —it only becomes detached when the operculum falls off, coming away along with it. In the single genus *Encalypta*, along with great uniformity in all other characters, there is great diversity in the structure of the peristome, which may be constructed either on the Haplolepidean or the Diplolepidean plan, and in the latter case the superposed exostome and endostome are sometimes coherent, owing to incomplete resorption of the horizontal walls of the peristome-forming cells. According to Philibert, *Encalypta* represents the synthetic ancestral type from which the Haplolepideæ and the Diplolepideæ have arisen.

(C). *Diplolepideæ*. In this group there are very few cleistocarpous forms, as compared with the Haplolepideæ, and to it belong the great majority of the Bryales, including practically all the pleurocarpous forms and some of the largest of the acrocarpous families. The peristome is double, very rarely apparently single or chambered (*Splachnum*, etc.) and still more rarely absent altogether. The exostome consists of sixteen teeth, sometimes joined in pairs, occasionally perforated or split; the outer layer consists of two series of membranes, the inner of a single series. The

endostome consists of very thin plates, the outer layer corresponding to the inner layer of the exostome. The thickened cell-walls that contribute to the formation of the entire peristome belong to three concentric layers of cells. As was shown by Philibert, the single peristome of the Haplolepideæ is the homologue of the inner peristome of the Diplolepideæ. It would therefore perhaps be better to apply the term "haplostome" to the simple peristome of the Haplolepideæ and to the inner peristome of the Diplolepideæ. The endostome of Diplolepideæ, however, presents much greater variety of form than does the simple peristome of Haplolepideæ; it sometimes consists of a single series of sixteen teeth, but in its typical form it is differentiated into a collar-like basal membrane (usually sharply folded or keeled), which bears on its margin a series of processes and between these a number of fine filaments or cilia. The Diplolepideæ are divided into two main series. (i.) *Epicranoideæ*. Exostome teeth superposed on the endostome processes; exostome teeth usually undivided, sometimes joined basally in pairs, sometimes joined at the tips to a small disc (e.g. *Funaria*), rarely all joined at the base to a narrow membrane; endostome not keeled, and lacking both basal membrane and cilia. The Epicranoideæ are again divided into (a) *Funariinæ* (Funariaceæ and Disceliaceæ) in which the endostome processes are free, and (b) *Splachninæ* (Splachnaceæ, Oedipodiaceæ, and Schistostegaceæ) in which the endostome is either absent or is coherent with the exostome. (ii.) *Metacranoideæ*. Exostome teeth alternating with the endostome processes; exostome teeth usually undivided, always free; endostome keeled and differentiated into basal membrane, processes, and cilia, but sometimes rudimentary and then occasionally united to the exostome, but rarely absent altogether. The Metacranoideæ, a very large group, are divided into (a) *Bryinæ* (Mitteniaceæ, Bryaceæ, Mniaceæ, Leptostomaceæ, Rhizogoniaceæ, Aulacomniaceæ, Timmiaceæ, Meeseaceæ, Bartramiaceæ, Spiridentaceæ); (b) *Isobryinæ* (Drepanophyllaceæ, Eustichiaceæ, Orthotrichaceæ, Erpodiaceæ, Cryphæaceæ, Leucodontaceæ, Pterobryaceæ, Fontinalaceæ, Climaciaceæ, Hedwigiaceæ, Meteoriaceæ, Sorapillaceæ, Neckeraceæ, etc.); (c) *Hookerinæ* (Nemataceæ, Pilotrichaceæ, Hookeriaceæ, Hypopterygiaceæ); (d) *Hypnobryinæ* (Fabroniaceæ, Entodontaceæ, Hypnaceæ, Brachytheciaceæ, etc.). These sub-divisions are based partly on minor characters of the peristome, partly on vegetative characters of the gametophyte.

LITERATURE OF TETRAPHIDALES, POLYTRICHALES, BUXBAUMIALES, AND EU-BRYALES.

(From the extensive literature on the higher Mosses, I have selected for citation here only the more important works dealing with the morphology of the groups mentioned; works relating to the vegetative organs and to the systematic and floristic study of Mosses are omitted, except in cases where they have a direct bearing upon the phylogeny of the Bryophyta in general and of the Mosses in particular).

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IX. INTER-RELATIONSHIPS OF THE HIGHER BRYOPHYTA (SPHAGNALES, ANDREÆALES, TETRAPHIDALES, POLYTRICHALES, BUXBAUMIALES, EU-BRYALES).

IN seeking for a starting-point for the evolution of the higher Bryophytes, or Mosses, one is struck by the remarkable resemblances between the Sphagnales on the one hand and the Anthocerotales and (to a smaller extent) the Jungermanniales on the other. Apart from the flat thalloid protonema, which suggests comparisons with both the lower Jungermanniales and the Anthocerotales, *Sphagnum* resembles the former group in the structure and dehiscence of its antheridium, and in the early development of the sporophyte. However, apart from the fact that in *Sphagnum* the young antheridium grows by an apical cell, instead of showing the intercalary growth characteristic of the Liverworts, it may be noted that in *Buxbaumia* the antheridium is very similar to that of *Sphagnum*. *Buxbaumia* is in many respects primitive, and it is interesting to note that in this genus the young leaf, instead of growing by an apical cell as in other Mosses, shows the bilobed condition characteristic of the Acrogynæ. It would appear that in *Sphagnum* the sexual organs and the leaves have departed from the intercalary mode of growth found in Liverworts, and show the apical cell growth found in the higher Mosses, but the sporogonium still undergoes intercalary growth and in its earliest stages presents a close resemblance to the embryo of Jungermanniales. The striking similarity between *Sphagnum* and the Anthocerotales in the origin and form of the archesporium suggests that *Sphagnum* has probably arisen from a synthetic ancestral type which combined

Jungermannian and Anthocerotean characters, and since the Anthocerotales diverge considerably from the other Liverworts, at any rate in the development and structure of the sporogonium, we might assume that the hypothetical primitive "Sphæro-riccia" type gave rise on one hand to the Sphærocarpales, Marchantiales, and Jungermanniales, and on the other to the Anthocerotales and Sphagnales. It must be admitted, however, that the gap between the Sphagnales and the Anthocerotales is much wider than that between the Anthocerotales and the other Liverworts. The four groups of lower Bryophytes (Sphærocarpales, Marchantiales, Jungermanniales, Anthocerotales) agree with each other, and differ from the higher Bryophytes, in the development of the sexual organs by means of intercalary growth and not by an apical cell, in having unicellular rhizoids, in the absence of an apical cell from the leaves in the case of foliose forms, and in the presence (except in Ricciaceæ) of sterile cells (typically developed as elaters) in the archesporium.

In the Bryales, the most striking advance upon the lower groups is the evolution of the peristome. If we assume that some at least of the cleistocarpous Bryales are primitive, it would be easy to trace from types like *Archidium* and *Phascum* a series of lines leading up to the typical Bryales, and this possibility should not be lost sight of. There has been a general tendency to regard these cleistocarpous genera as reduced, but in the writer's opinion the question of their position and affinities is quite as open as in the case of the Ricciaceæ. However, setting aside these doubtful forms, the genus *Andreæa* appears to point to a possible connecting-link between Sphagnales and Bryales, and also to throw some light upon the origin of the peristome. In *Andreæa*, the archesporium, though arising in the outermost zone of the endothecium, is completed above—just as in *Sphagnum* and Anthocerotales—by a zone of tissue extending across the entire endothecium, so that the columella is incomplete and is covered above by the dome-like archesporium.

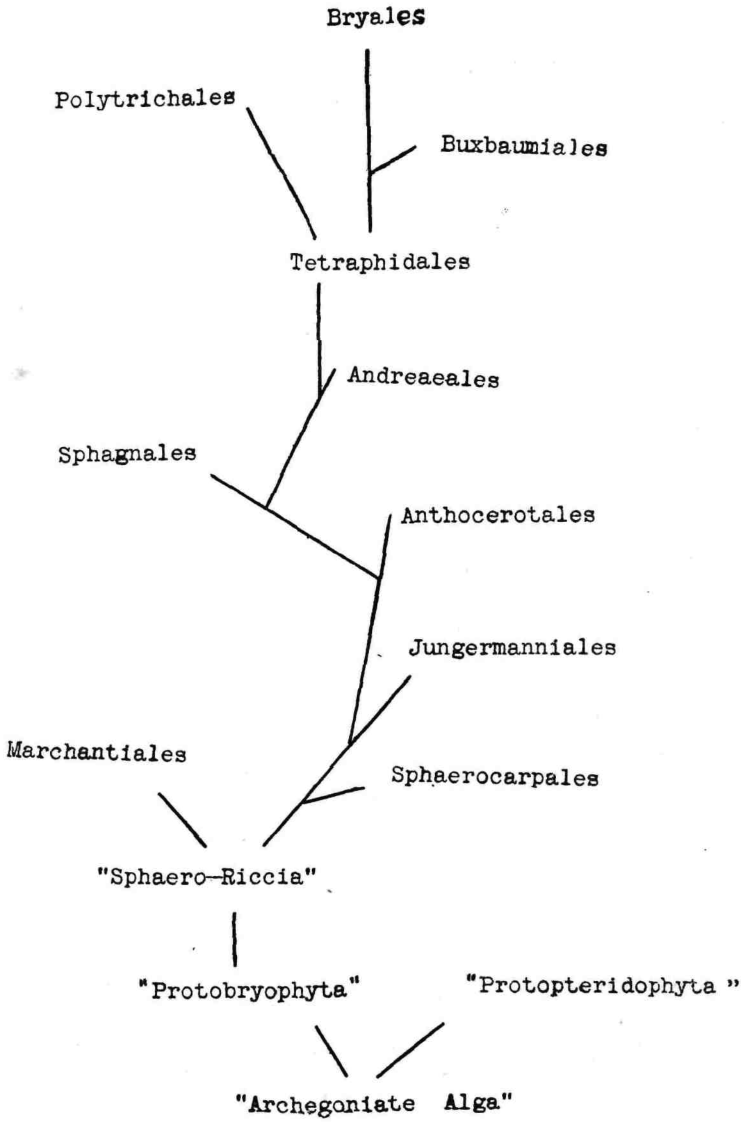
In the writer's view, there appears to be a definite correlation between the form of the archesporium and the fate of the apical tissue of the capsule. When the archesporium is dome-shaped, the sterile apical tissue is practically cut off from the stream of food materials brought upwards from the gametophyte, through the conducting-strand of the seta and thence through the columella of the capsule, and these materials are almost entirely used up in the

nutrition of the developing spores. This suggestion appears to be supported by a variety of facts in the morphology of the capsule in the lower Bryophytes. In these plants (Sphærocarpales, Marchantiales, Jungermanniales) the archesporium is a cell-mass derived from the entire endothecium, and in the great majority of cases sterilisation is confined to the formation of elaters, the amphithecium giving rise to the capsule-wall; but sometimes an imperfect columella of sterile tissue is formed (e.g., *Pellia*, *Aneura*) and there is some evidence that the endothecium may contribute to the formation of a lens-like cap or apical thickening of the capsule-wall (e.g., *Reboulia* and some other Marchantiales). In these lower Bryophytes, the elaters serve to nourish the developing spores, and after becoming thickened and losing their original contents they act as conductors of water and dissolved salts, finally assisting in spore dispersal at dehiscence of the capsule. As sterilisation became more definitely localised and complete in the central region of the capsule tissue, the elaters would become less important for the nutrition of the developing spores, and in the higher Bryophytes they have disappeared altogether. The absence of elaters in the Mosses may be correlated with the provision of dehiscence mechanisms which ensure the gradual dispersal of the spores through relatively small apertures. In most of the non-operculate (cleistocarpous) Bryales, the capsule is sessile or has a very short seta, and is shorter than the leaves which surround it, hence when the spores are set free by irregular rupture or decay of the capsule-wall they do not fall in a mass to the soil, the leaves acting functionally like a peristome and forming narrow spaces through which the spores may be gradually dispersed by wind or rain; in most of these forms the spores are relatively large and few. In some cleistocarpous Bryales, however, there is a well-developed seta (e.g., *Phascum*) which may attain a considerable length (e.g., *Voitia*), and in these forms the spores are usually much smaller than in cleistocarpous species with sessile or almost sessile capsule; in *Phascum*, etc., the capsule becomes detached from the seta, leaving a basal aperture through which the spores escape gradually when the capsule falls away, while in *Voitia* the entire sporogonium becomes detached, and the spores apparently escape (after rupture or decay of the capsule-wall) through a slit in the relatively large and persistent calyptra. A similar condition occurs in *Calymperes*, in which the persistent calyptra opens by several longitudinal slits. In all cases, there is a mechanism of some kind for gradual spore

dispersal, and this attains its highest development in the typical double peristome of the Diplolepideæ, the dominant Moss group and the culminating point of Bryophyte evolution. Comparison of a large number of Bryales shows that in general there is a definite relation between the size of the spores and the diameter of the apertures between the endostome processes and cilia—the smaller the spores the more numerous and completely developed are the cilia of the endostome.

In the higher Mosses, the tubular or barrel-like form of the archesporium, which is open above and below, allows ready passage of food materials to the apical region of the capsule, and in this region considerable growth occurs, leading to the development of annulus, operculum, and peristome. We may perhaps assume that the *Tetraphis* type of peristome is the most primitive, and that it is derived from that seen in those species of *Andreæa* in which the slits in the capsule-wall extend to the apex of the capsule and thus lead to the formation of a series of teeth. In Tetraphidaceæ the entire tissue of the capsule apex takes part in the formation of the simple peristome, the epidermal layer itself separating from the underlying tissue to form an operculum only after it has become slit into four lobes at the base. In the Polytrichales, we find that the development of the peristome is confined to a zone of amphithecial cells surrounding the columella; in the more primitive *Dawsonia* type this zone is several cells deep, while in the more advanced *Polytrichum* type it is limited to a single layer of cells. In the *Buxbaumia* type, again, the peristome-forming zone is broad, and the number of teeth forming the exostome is indefinite, these teeth being arranged in several concentric series. Finally, in the Eu-Bryales the peristome arises in a sharply defined zone of amphithecial cells and the teeth are always in two series. Along with this limitation of the peristome-forming zone to fewer and fewer layers of cells, we find a transition from the primitive *Tetraphis* type in which the peristome teeth consist of cell-masses to the *Bryum* type in which it consists solely of the remains of thickened and persistent cell-membranes.

The phylogenetic views thus briefly and tentatively put forward may be expressed diagrammatically in the accompanying table.



Phylogeny of the Bryophyta.

X. CLASSIFICATION OF THE BRYOPHYTA.

Since various modifications in the generally accepted classification of the Bryophyta have been suggested and discussed in the preceding pages, it will be convenient to set out here a table showing the proposed divisions of this phylum, with an enumeration (except in the case of the Eu-Bryales) of the families included in each of the ten divisions (Orders). The characters of these ten divisions have been given in some detail already, and are therefore not repeated here.

I. **Sphærocarpales.**

Sphærocarpaceæ.—*Sphærocarpus, Geothallus.*

Riellaceæ.—*Riella.*

II. **Marchantiales.**

Ricciaceæ.—*Riccia, Tessellina.*

Corsiniaceæ.—*Corsinia, Boschia.*

Targioniaceæ.—*Targionia, Cyathodium.*

Monocleaceæ.—*Monoclea.*

Cleveaceæ (Astroporeæ).—*Clevea, Sauteria, Peltolepis, Gollaniella.*

Aytoniaceæ (Operculatæ).—*Plagiochasma, Reboulia, Neesiella, Cryptomitrium, Grimaldia, Massalongoa, Fimbriaria.*

Marchantiaceæ (Compositæ).—*Exormotheca, Fegatella, Wiesnerella, Dumortiera, Monoselenium, Lunularia Preissia, Bucegia, Marchantia.*

III. **Jungermanniales.**

Aneuraceæ.—*Aneura, Metzgeria, Podomitrium, Umbraculum.*

Blyttiaceæ.—*Blyttia, Mörckia, Symphyogyna, Makinoa.*

Codoniaceæ.—*Pellia, Calycularia, Blasia, Cavicularia, Noteroclada, Petalophyllum, Fossombronia, Treubia.*

Calobryaceæ.—*Calobryum, Haplomitrium.*

Lophoziaceæ.

Cephaloziaceæ.

Ptilidiaceæ.

Scapaniaceæ.

Radulaceæ.

Pleuroziaceæ.
Porellaceæ.
Lejeuneaceæ.

IV. **Anthocerotales.**
Anthocerotaceæ.—*Anthoceros, Notothylas, Megaceros, Dendroceros.*

V. **Sphagnales.**
Sphagnaceæ.—*Sphagnum.*

VI. **Andreæales.**
Andreæaceæ.—*Andreæa.*

VI. **Tetraphidales.**
Tetraphidaceæ.—*Tetraphis, Tetradontium, Calomnium.*

VIII. **Polytrichales.**
Dawsoniaceæ.—*Dawsonia.*
Polytrichaceæ.—*Polytrichum, Catharinea, Lyellia,* etc.

IX. **Buxbaumiales.**
Buxbaumiaceæ.—*Buxbaumia.*
Diphysciaceæ.—*Diphyscium.*

X. **Eu-Bryales.**

The old-established primary division of the Bryophyta into the two classes Hepaticæ (including the first four of the Orders enumerated above) and Musci has only been called in question in connexion with the two groups Anthocerotales and Sphagnales. It is of interest to note that in certain of the characters which have been used to exclude the Anthocerotales from the Hepaticæ on one hand, and the Sphagnales from the Musci on the other, these two aberrant groups show a striking resemblance to each other. If the Anthocerotales are to be made a separate class apart from the Hepaticæ, either Sphagnales should also be considered a separate class apart from the Musci, thus making four primary divisions of Bryophyta—Hepaticæ proper, Anthocerotes, Sphagna, and Musci proper—or the Anthocerotales and Sphagnales might be united to form a class intermediate between the "Eu-Hepaticæ" and the "Eu-Musci," thus giving three classes of Bryophyta. The most striking character which is common to Anthocerotales and Sphagnales, as compared with the remaining Bryophyta, is the origin of the archesporium as a dome-like layer formed chiefly from the amphithecium and completed above across the endothecium, the columella—covered by

the archesporium—being derived from the endothecium. On the other hand, however, Anthocerotales and Sphagnales are separated by differences in the development of the sexual organs, and it would appear that these differences are absolutely characteristic of the two generally recognised divisions of Bryophyta. In all Hepaticæ that have been investigated, both the antheridium and the archegonium show intercalary growth, while in all Musci the young sexual organs grow by means of an apical cell. This generalisation has been challenged by Gayet, who claims that in all the groups of Bryophyta, excepting Anthocerotales, an active apical cell is present which produces the neck-cells but not the canal-cells, the latter being formed from the same mother-cell as that which gives rise to the oosphere and ventral canal-cell. According to Gayet, *Anthoceros* is the only Bryophyte in which the entire growth of the archegonium is intercalary. Campbell has pointed out that Gayet's methods are quite inadequate for the purpose of deciding this somewhat difficult question, and the results of the comparatively few recent researches in which the development of the archegonium has been carefully followed have shown that in Hepaticæ (including Anthocerotales) the archegonium does not at any stage grow by means of an apical cell, while in Mosses (including *Sphagnum*) an apical cell is present, its segments giving rise to the entire neck and its canal-cells.

In the writer's opinion, if any departure at all is to be made from the customary classification of the Bryophyta into Hepaticæ and Musci, it would be better to divide the whole phylum into the ten independent groups enumerated above, without setting the Anthocerotales and the Sphagnales apart from the remaining Hepaticæ on one hand and the remaining Musci on the other.

of the Vascular Plants. It has been suggested that the *Anthoceros* type of sporogonium forms a practicable starting point for the evolution of the Pteridophyta, but there are very great difficulties in the way of accepting such a hypothesis, which postulates the origin of roots and leaves from a sporogonium in the face of the fact that no known Bryophyte shows the slightest tendency to the development of such organs—unless, indeed, we may regard the foot of the typical Bryophyte sporogonium as a potential root, and the apophysis of Mosses like *Polytrichum* as a potential leaf.

If we adopt the view that the sporophyte generation originated as a free-living thallus, which later became hemmed in and retained in the parent plant, we are at once freed from these difficulties. However, it appears to the writer that the balance of evidence is distinctly in favour of the view that the Bryophyte sporogonium had an antithetic origin. In the general "pedigree table" on p. 194 indicating the writer's general conclusions regarding the inter-relationships between the main groups of Bryophyta, expression is given to the suggestion made by Mr. Tansley that the "Archegoniate Algæ" from which the primitive Bryophytes arose also gave rise to the primitive Pteridophytes, because this appears preferable to the view that the Pteridophytes arose from the Anthocerotales or other highly differentiated Bryophytes.

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ERRATUM.

Page 83, Line 4 from top, read "gradual" for "general."

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